AN AUTECOLOGICAL STUDY OF BUSHBUCK AND COMMON DUIKER IN RELATION TO FOREST MANAGEMENT

by

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PREFACE

The experimental work described in this thesis was carried out from the Institute of Natural Resources, University of Natal, Pietermaritzburg under the supervision of Professor J. Hanks, from July 1980 to June 1986.

This thesis, unless specifically indicated to the contrary in the text, is my own original work. It has not been submitted in any form to another university.

ABSTRACT

Frequent reports of damage caused by bushbuck and common duiker browsing on commercially important timber seedlings, and an interest in the potential and feasibility of hunting these two species on State land were the primary factors responsible for the Directorate of Forestry's motivation of this study. The study area at Weza State Forest comprised approximately 21 000 ha of plantations, grasslands and indigenous forests which were considered representative of timbered areas throughout the Natal midlands.

Several methods of age determination were investigated and these findings permitted assessments of growth, fecundity and population structure. The physiological condition of both antelope species was examined in relation to age, sex, reproduction and management strategies, and the results discussed in conjunction with mortality patterns. Principal foods of both bushbuck and duiker were determined from rumen analyses while 112 marked animals were regularly monitored to facilitate assessments of habitat selection and levels of spatial and social organisation. Estimates of the abundance of these largely solitary and nocturnal antelope were influenced by local movements in response to the availability of food and cover which varied seasonally and also fluctuated dramatically with forest succession and timber management activities.

Although bushbuck and duiker bred throughout the year and had almost identical rates of reproductive performance, different factors were responsible in limiting the sizes of these two populations. All the available evidence gathered in this study indicated that food resources during winter and early spring were inadequate for bushbuck, particularly in 1983 when 33% of the marked population died from starvation and/or exposure. Notable differences in forage utilization and habitat selection inferred little interspecific competition at this time of the year. In contrast, territorial duiker appeared to be susceptible to highly localised habitat modifications (including the availability

of food and cover) which occurred throughout the year and resulted from silvicultural and timber harvesting practices.

Rumen analyses and quantitative damage assessment surveys revealed that browsing on timber seedlings was usually confined to localised areas during the winter months and was much less severe than had been originally suggested. Conifers were regarded as a starvation food and methods of reducing damage to these young trees were recommended for potential problem areas.

Both antelope species were considered overabundant at Weza and recommendations for the future management of these populations included the limited utilization of surplus animals, by sport hunting on a sustained yield basis, and methods of manipulating and improving forest habitats.

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The Directorate of Forestry provided considerable support at Weza; I am particularly indebted to Mr. J.T. Nel

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CHAPTER ONE
INTRODUCTION

1.1 BACKGROUND TO THIS STUDY

In accepting the World Conservation Strategy (IUCN 1980), conservation today can no longer be concerned with wildlife alone; it is concerned with agriculture, fisheries, forestry, genetic resources - in essence with all micro-organisms, plants and animals and with the abiotic elements of the environment on which they depend (Allen 1980). In addition, conservation (as defined by the World Conservation Strategy) and preservation can no longer be regarded as synonyms; conservation includes preservation but also involves maintenance, sustainable use, restoration and enhancement of the environment (Allen 1980).

The World Conservation Strategy has obviously been adopted by the South African Government which recently published a national policy regarding environmental conservation (Department of Water Affairs, Forestry and Environmental Conservation 1980). With regards to nature conservation, this policy states:

> "By nature conservation is meant the management by man of renewable natural resources for his benefit and enjoyment, in order to ensure the survival and sustained yield of such resources, particularly ecosystems and their fauna and flora.
>
> These objectives may be achieved by:
>
> The co-ordination of the establishment, control and management of national and provincial parks, wilderness areas, nature reserves, declared mountain catchment areas or any other area worth conserving for the conservation of aquatic ecosystems including tidal rivers, marine habitats and islands, terrestrial ecosystems with

representative examples of veld types or plant communities and animal communities, special plant or animal communities and habitats for threatened plant and animal types, and outstanding natural phenomena;

The controlled utilisation of fauna and flora for man's benefit and enjoyment and;

Co-ordinated research."

Clearly, this policy differs radically from previous and more traditional philosophies, particularly with respect to the controlled utilisation of natural resources, and has subsequently been implemented in part by several government agencies. Outdoor recreational amenities, including hiking and fishing, are now available on State land. (Such amenities have, however, existed in areas administered by Provincial conservation authorities for some time). But there is a growing demand for the provision of additional facilities, particularly sport hunting, to be included in this multiple land use approach.

1.1.1 The Availability and Potential for Hunting in South Africa and Natal

Two factors are largely responsible for this increasing demand for suitable hunting areas on State land. The first is that through enlightened education of both hunters and the public, and as a result of voluntary legislation concerning the licensing, control and conduct of professional operators, hunting in South Africa has become socially more acceptable, and consequently more popular as a recreational pursuit. The second factor concerns the availability of hunting in South Africa. Although numerous game ranches have been established since the 1960's to cater for hunting and other forms of wildlife utilisation (Berry 1974), these are largely patronised by foreign sportsmen, particularly since the closure of the more traditional and well publicised hunting

areas of East Africa. This influx of overseas hunters, the capital invested in game ranches, and the type of hunting on offer (the choice of species available often depends on the predetermined length of the hunting safari), have all contributed to escalating hunting tariffs.

More recently, recreational hunting, at less competitive prices, has been made available to South African residents by the creation of public hunting areas in the Orange Free State and Transvaal. Essentially, these are equivalent to the controlled hunting areas of Zambia, Zimbabwe and Botswana (von Richter and Butynski 1974) and are administered by the respective Provincial conservation authorities. However, these facilities are absent in Natal, and hunting, except for the commercial game ranches, is confined to farmland where (as in western Europe) legally restricted hunting rights are associated with land tenure. Thus, unless a hunter is a landowner, or is invited by a landowner to hunt on his land, he must compete with professional organisations for his recreation.

Attempts to rectify this state of affairs in Natal led to discussions between the Natal Hunters and Game Conservation Association and the Directorate of Forestry, and in conjunction with the Directorate of Forestry's revised policy regarding nature conservation, contributed to the original motivation for this study.

1.1.2 Protection of Commercial Timber Species

In 1973 it was estimated that a 320% increase in the area currently afforested would be necessary to meet the South African demands for softwood timber by the year 2 000 (Kramwinkel 1973 cited in Marsh 1978). This represents an increase in area from 565 000 ha to 1 800 000 ha (approximately 45 740 ha per annum). In addition, the existing plantation area of hardwoods would have to increase by 160% during the same interval, amounting to a combined increase of 2 620 000 ha of afforestation (Marsh 1978).

However, the area receiving adequate rainfall for silviculture constitutes less than 10% of the Republic. In addition, this high rainfall area already accommodates existing plantations, farmlands and homelands, and consists partly of shallow, rocky soils unsuited to any type of cultivation. It is, therefore, highly improbable that afforestation at this predicted level of intensity will ever be realised.

Consequently, alternative methods of increasing timber yields must be sought. Research priorities pertaining to these goals have been identified and include tree and silviculture improvement, site research, compatibility between timber species and available sites, and forest protection (Directorate of Forestry 1983; Forestry Council 1983).

The control of problem animals and pests falls within the forest protection aspect, and although damage to timber species caused by browsing ungulates is a widespread problem (e.g. Bergerud and Manuel 1968; Campbell 1974; Mitchell et al. 1977; Black et al. 1979; Brodie et al. 1979; Yanchinski 1982), economic losses are likely to escalate as more marginal areas become afforested. The Directorate of Forestry's concern regarding wildlife utilisation of commercially important timber species was partially responsible for prompting this study.

1.1.3 Wildlife Management in Timber Plantations

Wildlife populations inhabiting forested areas have received little, if any, attention since these plantations were established. Management has largely been based on a policy of total preservation, with the result that the relevant authorities are largely ignorant of population trends, abundance, and in some instances, actual occurrence. Further, the effects of forestry management practices on wildlife populations, and how these may be positively modified, are unknown.

The need for detailed research into these aspects is obvious, and will increase as activities associated with timber management and recreational use in forested areas intensify. This required research, which has been recognised by the Directorate of Forestry for several years, forms the basis of this study.

Several mammal species have adapted to the environmental conditions created by exotic timber production in South Africa. Among these, the bushbuck (Tragelaphus scriptus) and the common duiker (Sylvicapra grimmia) are probably the most numerous and successful (Mentis 1973a, 1973b, 1974; Smithers 1983). The abundance of these two species, together with the damage they cause by browsing on commercial seedlings (von Breitenbach 1974; de Zwaan 1977; Schutz et al. 1978; Sommerlatte 1979 cited in Smithers 1983; Novellie and Bigalke 1981; R. Collinson, pers. comm.; D. Rowe-Rowe, pers. comm.; G. van den Bussche, pers. comm.; R. Walter, pers. comm.) and their popularity among hunters in providing high quality hunting, made bushbuck and duiker obvious species for research in this applied ecological study.

1.2 TAXONOMY

1.2.1 Bushbuck

The classification of the bushbuck, following Ansell (1971), is:

Family	:	Bovidae
Subfamily	:	Bovinae
Tribe	:	Tragelaphine
Genus	:	Tragelaphus
Species	:	scriptus

Haltenorth (1963) listed 23 subspecies while Ansell (1971) provisionally accepted only nine of these, largely on grounds of geographical distribution:

T. s. scriptus (Pallas 1776) from Senegal eastwards to Nigeria and southwards to the central Congo;

T. s. bor (Heuglin 1877) which occurs in Chad, Central African Republic, northern Congo, southern Sudan, Uganda and northwestern Kenya;

T. s. decula (Ruppell 1835) and T. s. powelli (Matschie 1912) which occur in the northwestern and central regions of Ethiopa respectively;

T. s. meneliki (Neumann 1902) from southern Ethiopa and Somalia;

T. s. delamerei (Pocock 1900) which is found in most of Kenya and Tanzania;

T. s. ornatus (Pocock 1900) which occurs in Angola, northeastern South West Africa/Namibia, northwestern Botswana, Zambia, southeastern Congo, Malawi, northern Mozambique and northeastern Zimbabwe;

T. s. roualeyni (Gordon-Cumming 1850) occurring in the Limpopo River drainage system (eastern Botswana, western and southern Zimbabwe, southern Mozambique, northeastern Zululand, eastern Swaziland and the Transvaal lowveld);

T. s. sylvaticus (Sparrman 1780) which occurs in central and eastern Natal/KwaZulu, Transkei and the coastal regions of the Cape Province.

Most authors agree on the number of Tragelaphine species, but opinions at the levels of subfamily, tribe and genus are at variance (Leuthold 1979). Ansell (1971) presents the Tragelaphines as follows:

Tribe : Tragelaphini
Genus : Tragelaphus
Subgenus : Boocercus
Tragelaphus eurycerus : Bongo

Subgenus	:	Tragelaphus		
		Tragelaphus buxtoni	:	Mountain Nyala
		Tragelaphus angasi	:	Nyala
		Tragelaphus spekei	:	Sitatunga
		Tragelaphus imberbis	:	Lesser Kudu
		Tragelaphus strepsiceros	:	Greater Kudu
		Tragelaphus scriptus	:	Bushbuck
Genus	:	Taurotragus		
		Taurotragus oryx	:	Eland
		Taurotragus derbianus	:	Giant Eland

Several authors consider that the Tragelaphines should be removed from the Bovinae and placed in a separate subfamily, Tragelaphinae (Walther 1964; Leuthold 1979), while hybrids between bongo and sitatunga (Tijskens 1968) and between kudu and eland (Boulineau 1933; Jorge et al.1976) are considered by van Gelder (1977) to be valid reasons for including all Tragelaphines in the single genus Tragelaphus.

Unless otherwise stated, this study refers to the South African bushbuck Tragelaphus scriptus sylvaticus. Comprehensive morphological descriptions of this and other subspecies are given in Roberts (1951), Dorst and Dandelot (1970), Ansell (1971), Hanks (1974), Zaloumis and Cross (1974), Wynne-Jones (1980) and Smithers (1983).

1.2.2 Duiker

There is less controversy concerning the taxonomy of the duikers, and Ansell's (1971) classification of the common duiker is generally accepted (e.g. Estes 1974) as follows:

Family	:	Bovidae
Subfamily	:	Cephalophinae
Genus	:	Sylvicapra
Species	:	grimmia

Haltenorth (1963) listed 19 subspecies from the continent, and these, with several modifications, have been

included by Ansell (1971) with reservations regarding their validity and limits of distribution. Six of these subspecies are included in the Southern African subregion of Smithers (1983):

S. g. grimmia (Linnaeus 1758) from the southern and western Cape Province;

S. g. burchelli (Smith 1827) from the eastern Cape Province and perhaps to Natal;

S. g. transvaalensis (Roberts 1926) which occurs in western Transvaal, eastern Botswana and southwestern Zimbabwe;

S. g. caffra (Fitzinger 1869) from northeastern Natal, eastern Transvaal, eastern Zimbabwe and southern Mozambique;

S. g. steinhardti (Zukowsky 1924) from South West Africa/Namibia and western Botswana;

S. g. orbicularis (Peters 1852) from central Mozambique.

Separation of the subfamily Cephalophinae into the two genera Cephalophus (the forest duikers) and Sylvicapra (the common or bush duiker) is generally accepted on both morphological and ecological grounds (Oboussier 1966; Ansell 1971; Estes 1974; Smithers 1983) and is given by Ansell (1971) as follows:

Genus : Cephalophus

Cephalophus monticola	:	Blue duiker
Cephalophus maxwelli	:	Maxwell's duiker
Cephalophus natalensis	:	Red forest duiker
Cephalophus callipygus	:	Peter's duiker
Cephalophus nigrifrons	:	Black-fronted duiker
Cephalophus zebra	:	Zebra duiker
Cephalophus niger	:	Black duiker
Cephalophus dorsalis	:	Bay duiker

	Cephalophus ogilbyi	:	Ogilby's duiker
	Cephalophus leucogaster	:	White-bellied duiker
	Cephalophus rufilatus	:	Red-flanked duiker
	Cephalophus adersi	:	Ader's duiker
	Cephalophus jentinki	:	Jentink's duiker
	Cephalophus spadix	:	Abbott's duiker
	Cephalophus sylvicultor	:	Yellow-backed duiker
Genus :	*Sylvicapra*		
	Sylvicapra grimmia	:	Common, grey or bush duiker

Unequivocal identification of the subspecies in this study is not possible due to the uncertain distributional limits of *S. g. burchelli* and *S. g. caffra*. Descriptions of the common duiker are detailed in Roberts (1951), Dorst and Dandelot (1970), Ansell (1971), Hanks (1974), Zaloumis and Cross (1974), Wynne-Jones (1980) and Smithers (1983).

1.3 DISTRIBUTION AND STATUS

The common duiker is the most widely distributed antelope species in Africa and is closely followed by the bushbuck (Mentis 1973a, 1973b). These distributions have been documented on a continental scale by Bigalke (1968), Ansell (1971), Kingdon (1982) and Smithers (1983), and are illustrated in Fig. 1.1.

Details of more regional distributions have been provided by numerous authors for southern Africa (Smithers 1966; du Plessis 1969; Hanks 1974; Zaloumis and Cross 1974); Zambia (Ansell 1960a, 1978); Botswana (Smithers 1971); Zimbabwe (Fraser 1958; Child and Savory 1964); Mozambique (Smithers and Tello 1976); South West Africa/Namibia ((duiker only) Joubert and Mostert 1975); South African (Knobel 1958); Transvaal (Kettlitz 1955, 1962; Rautenbach 1982); Cape Province (Bigalke and Bateman 1962); Orange Free State ((duiker only) van Ee 1962) and Natal (Vincent 1962; Mentis 1974; Howard and Marchant 1984).

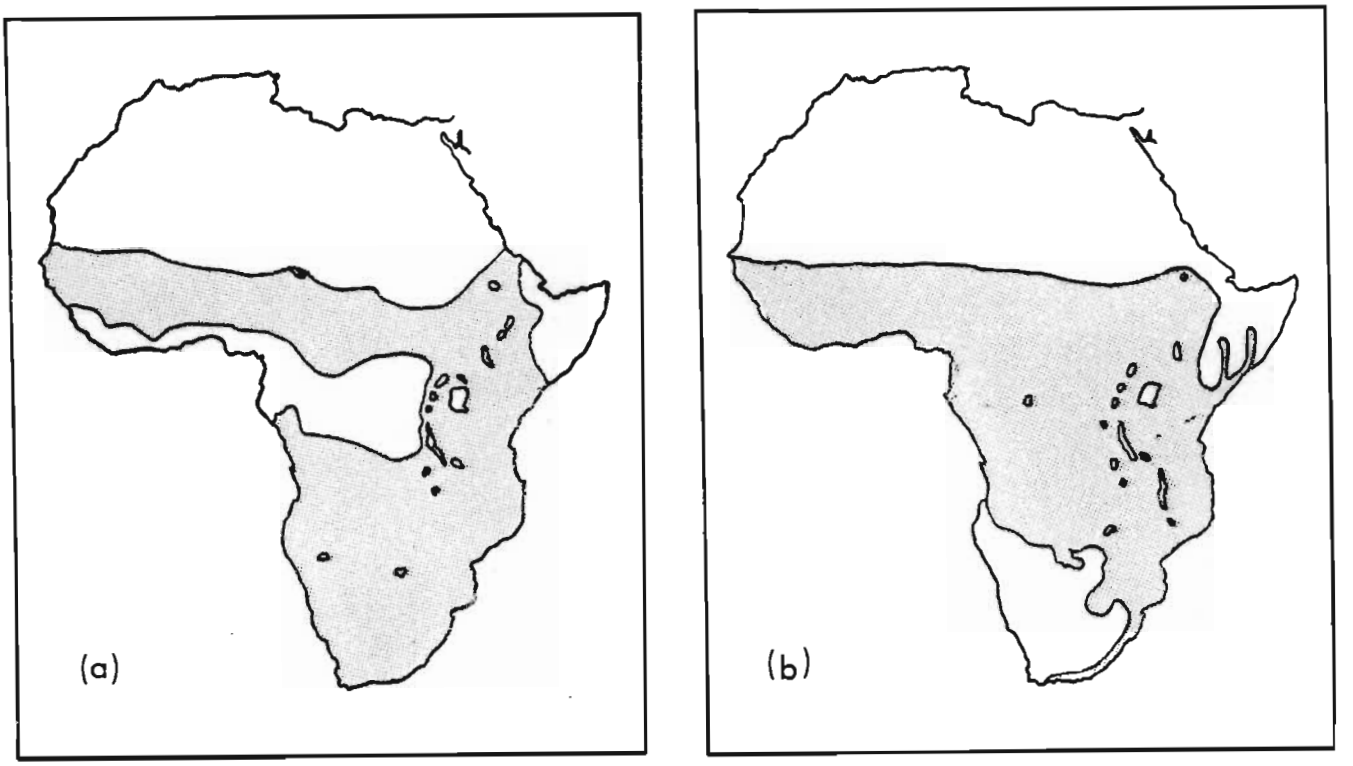


FIGURE 1.1 The distribution of a) common duiker and b) bushbuck in Africa (after Smithers 1983)

As inferred by its wide distribution, the common duiker is catholic in its habitat requirements and is not confined to any particular vegetational association (Ferrar and Walker 1974; Pienaar 1974; Evans 1979; Smithers 1971, 1983). Although it is typically a savanna species, it also occurs in quite open country except where the vegetation is too short to provide sufficient cover (Dorst and Dandelot 1970; Ansell 1971; Smithers 1971; Mentis 1973a). Forests are avoided by the common duiker; it is replaced by the blue duiker in forested habitats in southern Africa (Smithers 1983).

The major factor influencing the gross distribution of the bushbuck is the presence of densely structured vegetation such as forests, thickets and riverine bush (Smithers 1966; Dorst and Dandelot 1970; Mentis 1973b; Pienaar 1974; Simpson 1974a). Bushbuck may be further localised by their dependence on, or preference for, areas where surface water is available (Ansell 1960a; Smithers 1971; Jacobsen 1974; Zaloumis and Cross 1974; Walker 1975; Smithers and Tello 1976; Okiria 1980; Rautenbach 1982; Smithers 1983).

Where knowledge on the factors influencing the gross distribution of bushbuck and duiker is important in the long term planning of land use for large areas (e.g. Cobb 1979), a different set of environmental factors affect dispersion at the local level. Such factors include food and nutrition, climate and weather, human disturbance, habitat requirements and preferences, and social and spatial organisation. These are considered in turn (and in relation to forestry management which takes place within relatively small areas) elsewhere in this study.

The conservation status of both bushbuck and common duiker appears to be satisfactory/secure throughout the majority of their ranges (Bere 1958; Bigalke 1958; Fraser 1958; Knobel 1958; Taylor 1958; Dorst and Dandelot 1970; Smithers 1971; Zaloumis and Cross 1974; Smithers and Tello 1976; Kingdon 1982), which have altered little from historical times (du Plessis 1969; Smithers 1983). Bothma (1975) considers bushbuck to be rare in South West Africa/Namibia (where their occurrence is restricted by the availability of suitable habitat, Bigalke 1958), and also in Swaziland where, in the eastern area, however, Smithers (1983) states the species is widespread.

Where bushbuck and duiker numbers have declined in localised areas during the last few years, these have largely resulted from habitat destruction (Grimwood and Benson 1958; du Plessis 1969; Smithers 1983), rather than over-utilisation, even though both species have been heavily exploited in certain regions for meat production (von La Chevallerie 1970; Ajayi 1971; Asibey 1974), or in tsetse fly control operations (Child and Wilson 1964; Riney 1964; Wilson and Child 1964; Wilson and Roth 1967; Mentis 1970; Morris 1973). The common duiker is particularly resilient to intensive hunting and where intraspecific and interspecific competition has been reduced through culling, this has resulted in a marked increased in population growth (Child and Wilson 1964; Wilson and Roth 1967).

This resilience to hunting, the ability of both species to exploit cultivated land where there is suitable cover (Bigalke 1958; Fraser 1958; Grimwood and Benson 1958; Smithers 1966, 1971; Dorst and Dandelot 1970; Zaloumis and Cross 1974; Smithers and Tello 1976; Rautenbach 1982), even in suburban areas (Kingdon 1982; Smithers 1983), their favourable response to bush encroachment (Smithers and Tello 1976) and some forms of habitat modification (e.g. exotic plantations and canelands, Mentis 1973a, 1973b, 1974), all contribute to their widespread distribution and secure conservation status.

The population status of these two species is rarely known however, even in well managed conservation areas (Brynard and Pienaar 1960; Pienaar 1963; Dixon 1964, 1966; Foster and Coe 1968; Bourquin et al. 1971; Bourquin and Sowler 1980; Rautenbach et al. 1981), largely because the nocturnal activities, relative densities and habitat preferences of bushbuck and common duiker do not lend themselves to conventional census techniques. Nevertheless, the inclusion of bushbuck males and common duiker within the schedule of ordinary game in Natal reflects their current conservation and population status in this Province, since unlimited numbers of these two species (and impala Aepyceros melampus) may be hunted by landowners and their associates for three months each year. Unfortunately, the numbers of ordinary game animals shot per annum are not recorded, as hunters are not required to furnish any details of their activities throughout the season. Female bushbuck are scheduled as protected game however, and may only be hunted by persons possessing the relevant permit or licence and on condition that details of all females shot are returned to the Natal Parks Board. Since the classification of bushbuck females as protected game is based more on traditional rather than scientific reasons (Mentis 1973c), there is a general reluctance in hunting them, and consequently their level of exploitation is relatively low (Mentis et al. 1978).

1.4 PREVIOUS STUDIES OF BUSHBUCK AND DUIKER

Although scientific interest in the bushbuck has steadily increased during the last few years, our present knowledge of the ecology of this species remains somewhat limited. Prior to this, most reports were largely of a general nature published in popular journals (Shaw 1947; Kolbe 1948; Duckworth 1948; Jackson 1955; Blower 1962; Burton 1963; Bainbridge 1973). Specific studies, including reproduction, growth, age determination and condition, only commenced when considerable numbers of bushbuck were shot during the tsetse fly control campaigns in Zambia and Zimbabwe (Wilson and Child 1964; Simpson 1971, 1972, 1973; Morris 1973; Morris and Hanks 1974). More recently, attention has been focused on bushbuck habitat preferences, feeding habits and social and spatial organisation (Allsopp 1970, 1978; Elder and Elder 1970; Jacobsen 1974; Simpson 1974a, 1974b, 1974c; Waser 1975a, 1975b; Odendaal 1977, 1983; Odendaal and Bigalke 1979a, 1979b; Okiria 1980).

The common duiker has received even less attention from biologists than the bushbuck, and again many of the pertinent studies concerning this ubiquitous antelope have arisen from tsetse fly control schemes. These include aspects of age determination and growth (Riney and Child 1960, 1964; Wilson et al.1984), reproduction (Wilson and Clarke 1962; Child and Mossman 1965; Symington and Paterson 1970; von Ketelhodt 1977), feeding habits (Wilson and Clarke 1962; Wilson 1966a), predators (Wilson 1966b), effects of hunting (Child and Wilson 1964; Wilson and Roth 1967), social organisation and behaviour (Hopkins 1966; Dunbar and Dunbar 1979), blood parasites (Keymer 1969) and drug immobilization (Wilson 1967).

These aspects are reviewed in detail within the relevant sections of this study.

1.5 OBJECTIVES OF THIS STUDY

The original proposals for a study of wildlife in plantation areas were issued by the Directorate of Forestry. These were restricted to the bushbuck and included a survey on hunting potential, a study of the general biology of this species, an assessment of habitat conditions and their possible modification, and a survey of the extent and possible control of damage to exotic timber seedlings. These aims were subsequently revised and an investigation which would explain the distribution and abundance of both bushbuck and duiker in plantation areas and serve as a basis for possible management for damage control and for other purposes, including cropping or hunting, was requested (F. Kruger, pers. comm.).

Following these guidelines, new project proposals were presented by the author at the inaugural meeting of the Weza Bushbuck and Duiker Steering Committee. This study, which was undertaken after the acceptance of these proposals in September 1980, has the following objectives:

(i) to determine the present status of bushbuck and duiker in plantation areas of Natal and to evaluate the precision, accuracy, and repeatability of population monitoring techniques;

(ii) to assess the distribution, movements and habitat preferences of these two species, their feeding ecology and level of interspecific competition;

(iii) to assess the extent to which these movements, habitat preferences and feeding strategies may affect, and be influenced by, forestry management practices;

(iv) to evaluate the proportions of these populations that may be utilised for sport hunting and/or meat production on a sustained yield basis;

(v) to provide recommendations for the future management of bushbuck and duiker occurring in State owned and private plantations, together with relevant details of the most effective and reliable techniques used to monitor these two populations; and

(vi) to record the presence of other mammal species encountered in indigenous forests and plantations during the course of this study.

CHAPTER TWO
STUDY AREA

2.1 INTRODUCTION

To meet the objectives outlined in Chapter One, it was necessary to conduct the study in an area which was State owned, was sufficiently large to be representative of the major types of forest vegetation and forms of forest management practices occurring in Natal, and which had unexploited populations of bushbuck and duiker. Consequently, Weza State Forest, which constitutes 60% of the afforested area administered by the State in the Natal Midlands (D. Stahl, pers. comm.), and which reputedly had high densities of both bushbuck and duiker (W. Bainbridge, pers. comm.), was selected as the study area. Intensive studies of bushbuck and duiker numbers, movements, social organisation, habitat preferences and responses to silvicultural and exploitation practices were largely confined to two adjacent areas, which are referred to as the intensive study areas (see section 2.9). Beyond these regions, studies involving the assessment of population structure, additional movements, culling for post-mortem analyses and browsing surveys were undertaken in the remaining plantation and accessible indigenous forests, which form the extensive study area. In addition, comparative post-mortem data and harvesting levels were obtained during the hunting season from numerous privately-owned plantations and farms adjacent to Weza State Forest.

2.2 HISTORY OF WEZA STATE FOREST

Weza State Forest originated in 1893 when the main indigenous forests of Ngele, Stinkwood, Mpetyne and Bangeni were formally demarcated. These forests were exploited at various levels of intensity until the 1940's when a total preservation policy was adopted. Restricted exploitation, involving the extraction and sale of dead and damaged trees

(particularly those species in high demand, such as yellowwoods (Podocarpus spp.) and stinkwood (Ocotea bullata)) has again been practiced during the last few years.

Afforestation commenced at Weza in 1902 and was largely confined to forest openings and margins. As additional land was acquired, two separate plantations (Weza and Border) were established in 1923 and 1929 respectively. A third plantation, Middlebrook, commenced in 1936 when the Department of Forestry purchased the land between Weza and Border. These three plantations were amalgamated in 1968, and with the purchase of additional adjacent areas in the 1970's, Weza State Forest became the largest State plantation in the Republic.

Afforestation commenced on a large scale in 1923, and the first sales of sawlogs from the plantation occurred in 1933. A local sawmill was erected in 1939 to process this timber, and during the first year of production had a log intake of 11 470 m^3. Escalating demands for timber resulted in the construction of a new, improved mill in 1941 and again in 1957. In response to additional timber production, and as a result of advanced technology, the present mill is capable of handling 103 700 m^3 of locally produced timber per annum (P. Fifield, pers. comm.). This represents approximately 65% of the annual volume of economic timber harvested at Weza State Forest (J.T. Nel, pers. comm.).

2.3 LOCATION AND TOPOGRAPHY

Weza State Forest, which is 21 700 ha in extent, is situated at the southern tip of Natal. Its western, southern and northern boundaries are part of the international border between South Africa and the Transkei. The north-eastern section of Weza abuts against private plantations and agricultural land owned by European farmers while the south-eastern area borders on to KwaZulu (Fig. 2.1).

The topography of the area is fairly rugged, rising from

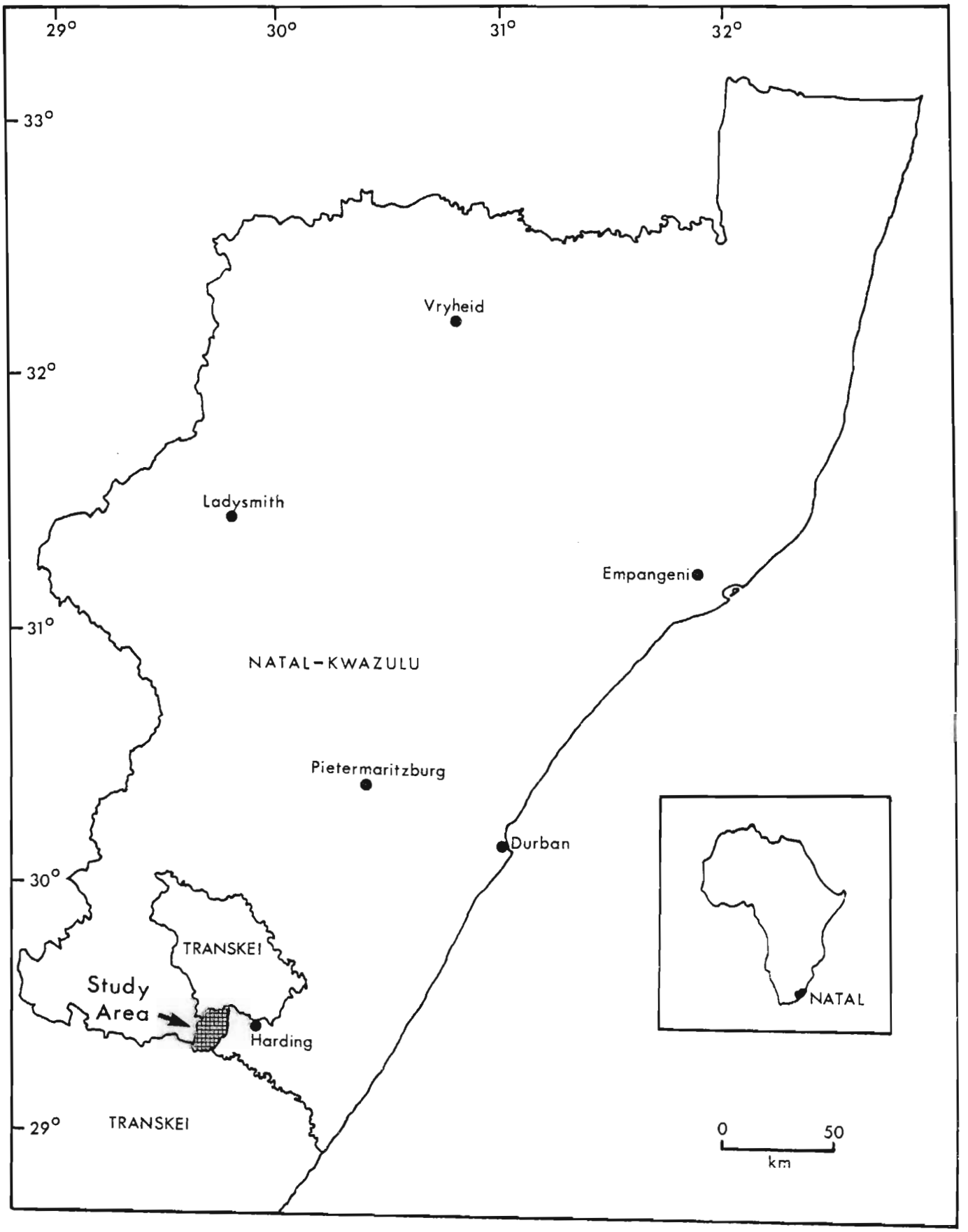


FIGURE 2.1 Location of the extensive study area in Natal-KwaZulu.

900 m above sea level in the east to 1 300 m above sea level in the central regions, and then increasing sharply to over 2 200 m above sea level where the long axis of the Ingeli Mountain range forms the western boundary (Fig. 2.2). Ridges of the foothills and the drainage therefore generally run in a west to easterly direction.

Numerous streams and rivers originate in the area. The Mafadobe river runs along the southern boundary to its confluence with the Mtamvuna, while the Weza river, with its tributary the Manzamnyama, are the major rivers in the north (Fig. 2.2). Almost all of the extensive water courses at Weza are perennial and two small streams have been dammed for recreational purposes in the less undulating regions of the north and east.

Representative areas of Weza State Forest were selected in the flatter terrain of the eastern section for intensive study purposes, mainly to facilitate travel, field observations and radio telemetry.

2.4 GEOLOGY

The majority of Weza State Forest is classified under the Karoo System, Ecca series and consists of alternating layers of soft shales and hard sandstones (Thorrington-Smith et al. 1978).

Numerous dolerite dykes and sills impregnated the sedimentary rocks of the Beaufort series in the Ingeli Mountain range and formed the ridges of the adjacent eastern foothills. Yellow and red apedal soils, which are freely drained and dystrophic, are typical of the area.

2.5 CLIMATE

Weza State Forest is situated in the summer rainfall area, and receives approximately 80% of the annual rainfall

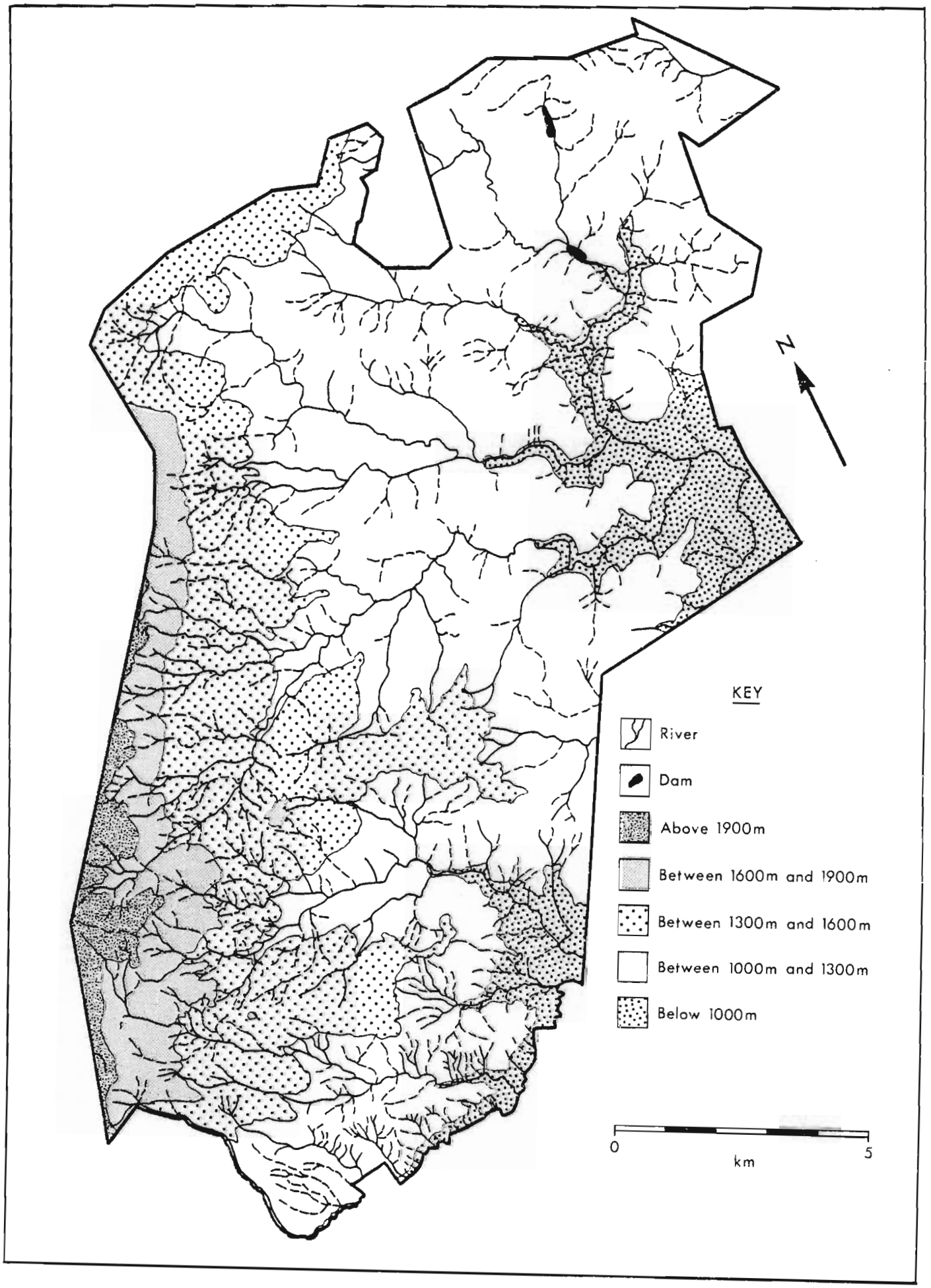


FIGURE 2.2 The main topographical features of Weza State Forest.

during the six months from October to March. This precipitation is largely in the form of numerous thunderstorms during the summer months, preceded by soft soaking rains during the spring, and followed by moderate autumn rains. Mist is common except in the winter months, when snow occasionally falls on the Ingeli Mountain range. The prevailing winds are from the north-east, with the rain bearing winds from the south-east to south-west. Dry interior winds from the north-west (berg winds) are common during the winter and drastically increase the fire hazard at this time.

The influence of the Ingeli Mountain range effectively separates Weza State Forest into two bioclimatic zones (Phillips 1973). The Highland Sourveld of the Ingeli Range has cool to mild summers and cool to cold (occasionally very cold) winters. The majority of Weza falls under the Midlands Mistbelt category, where the potential climax vegetation is mistbelt forest and thicket in the central regions and a minor area in the east of upland forest and thicket. Both regions have mild to cool summers and cool to cold winters, when severe frosts are common, particularly in the low-lying areas. The mean annual temperature at Weza is approximately 13°C (Schulze 1982).

The entire study area is classified as humid to subhumid (Phillips 1973) with a humidity index of 0,94 (Marsh 1978).

Daily rainfall and maximum and minimum temperatures have been recorded at Weza State Forest since 1927 and 1980 respectively. Mean monthly values, based on these data, are summarised in Fig. 2.3, while the maximum and minimum monthly rainfall values during this 53 year period are illustrated in Fig. 2.4. The mean annual rainfall prior to the commencement of this study was 1054,6 mm, while the mean annual rainfall measured from June to May (i.e. incorporating the entire rainfall season) was 1041,0 mm.

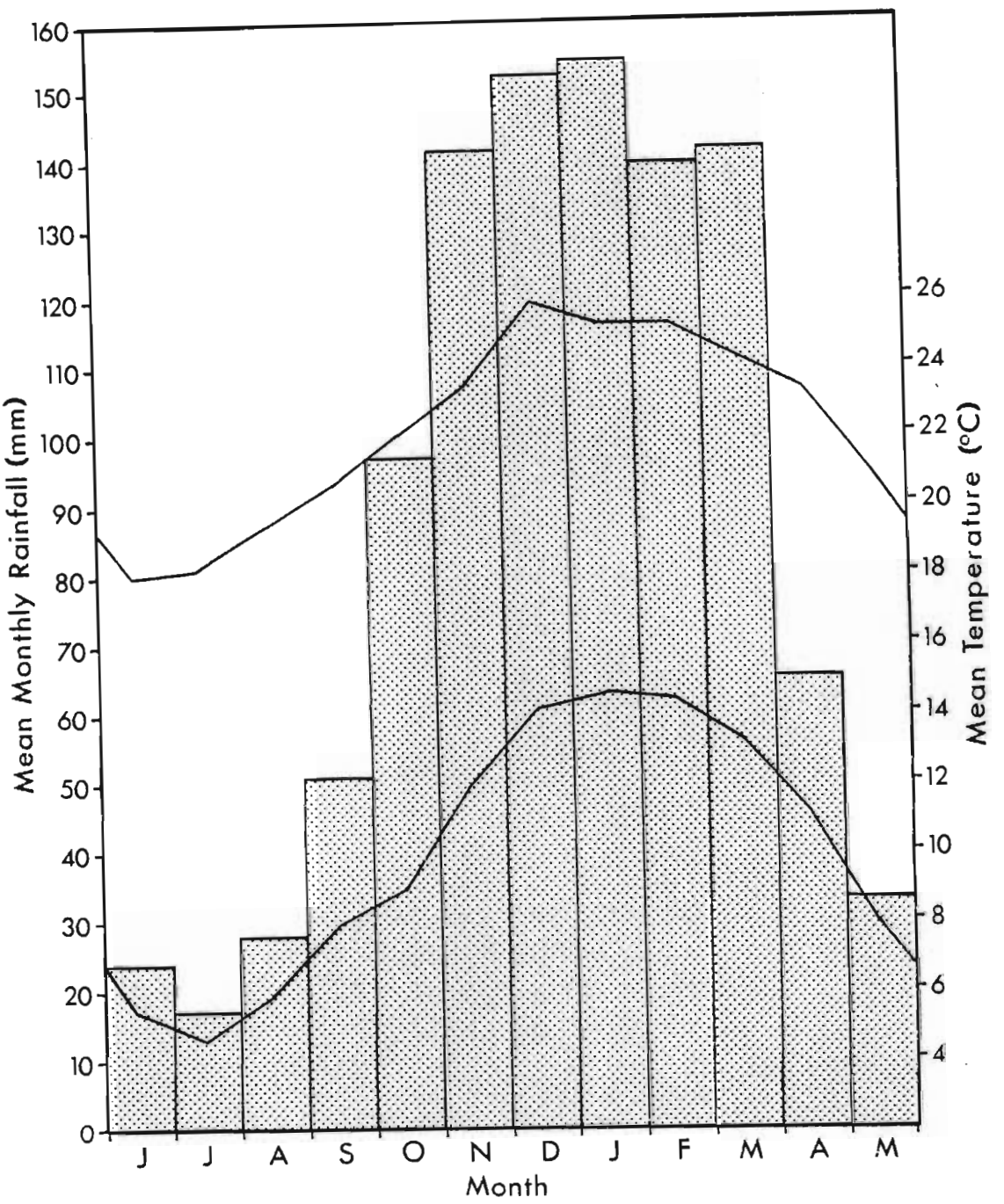


FIGURE 2.3 The mean monthly rainfall (1927-1979) and mean monthly maximum and minimum air temperatures (1980-1984) at Weza State Forest.

Months receiving above average, average or below average rainfall during the course of this study are illustrated in Fig. 2.5, where actual rainfall is expressed as a percentage of the mean rainfall for that month during the years 1927 to 1979. Annual rainfall (June to May) during the study was

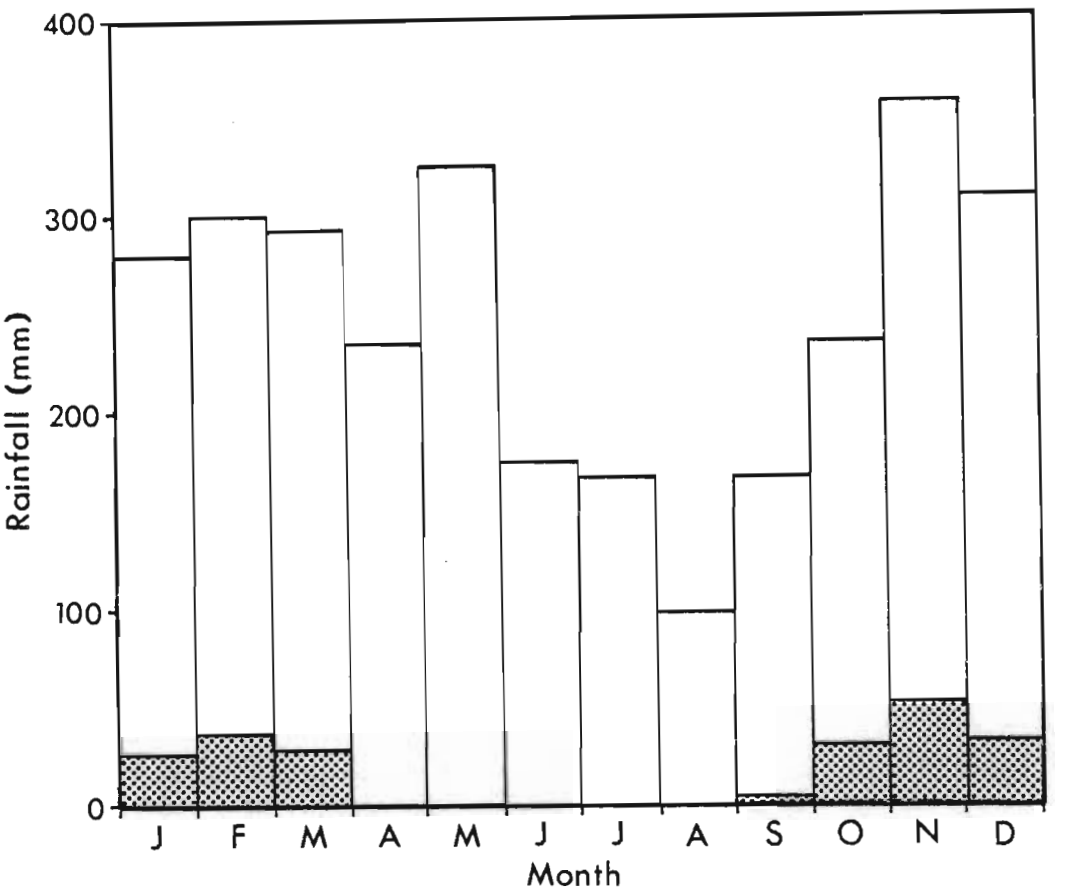


FIGURE 2.4 Maximum and minimum (stippled) monthly rainfall at Weza State Forest (1927-1979).

below average during the 1979 to 1980, 1981 to 1982 and 1982 to 1983 seasons, close to average during 1980 to 1981, and above average during the last year of study in 1983 to 1984 (Table 2.1).

All of these figures are based on records obtained at Weza Village on the eastern boundary. Four other weather stations are maintained within Weza State Forest, and records from these indicate that up to 150% of the annual precipitation recorded at Weza Village is received in the central, southern and western regions, while the northern areas receive approximately 95% of the rainfall measured at the Forestry offices in Weza. Other climatic data recorded at the Forestry Offices are summarised in Table 2.2.

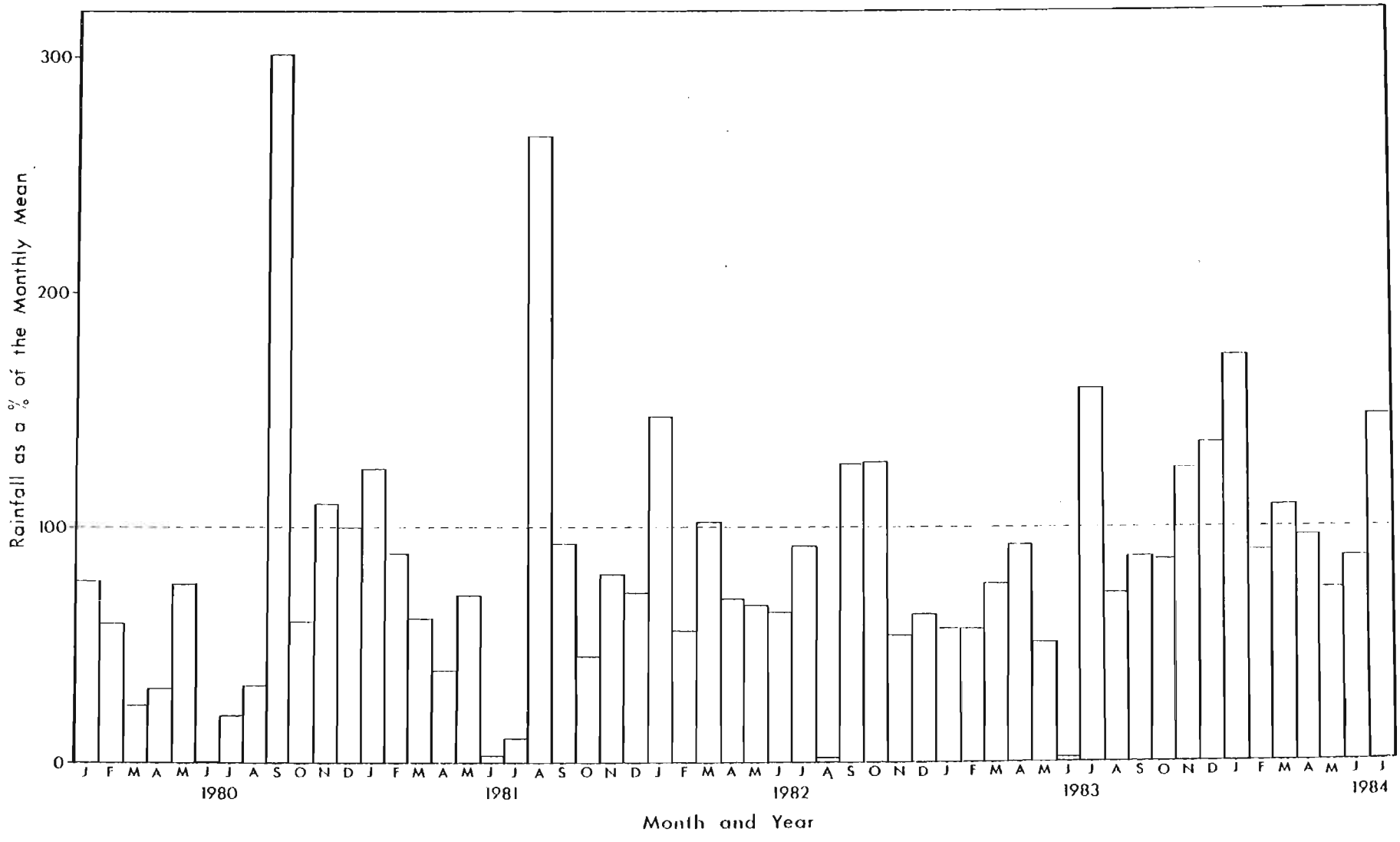


FIGURE 2.5 Monthly rainfall during the study period (July 1980 to July 1984) expressed as a percentage of the mean monthly rainfall (1927-1979).

TABLE 2.1 Precipitation recorded at Weza during the five rainfall seasons 1979-1980 to 1983-1984.

Rainfall season	Rainfall	Rainfall as a % of the mean rainfall season 1927-1979
1979-1980	745,4mm	71,6%
1980-1981	987,8mm	94,9%
1981-1982	910,7mm	87,5%
1982-1983	753,8mm	72,4%
1983-1984	1202,5mm	115,5%

TABLE 2.2 Monthly rainfall and temperature variables at Weza State Forest.

Variable	Month											
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Mean no. of days with rain	1,6	2,0	5,2	9,8	12,2	15,1	15,6	15,9	13,9	14,1	8,3	4,3
Mean no. of days with rain > 10mm	0,3	0,3	0,5	1,5	2,5	5,8	4,3	4,8	2,8	3,4	1,4	1,0
Mean monthly occurrence of thunderstorms (days)	0,1	0,1	1,7	2,9	5,1	6,7	6,1	7,0	4,9	5,6	2,9	0,8
Mean difference in range of daily min. and max. temperatures (°C)	10,6	11,6	11,5	10,7	11,1	9,5	9,7	8,6	8,7	9,0	10,2	10,9
Mean differences in the range of monthly max. temperatures (°C)	15,3	13,8	16,3	19,5	21,8	19,5	18,5	18,0	14,3	17,3	14,8	15,3
Mean differences in the range of monthly min. temperatures (°C)	10,8	11,0	12,3	13,3	14,0	12,3	12,3	8,8	10,8	10,3	10,3	13,0
Mean differences in the max. range of monthly temperatures (°C)	23,8	23,8	25,0	27,3	29,0	24,5	23,5	22,5	20,8	21,8	21,8	24,0
Mean differences in the min. range of monthly temperatures (°C)	4,5	4,3	3,8	2,5	3,8	1,8	4,0	2,4	2,8	1,5	3,0	3,5

2.5.1 Definition of Seasons

Seasons in temperate regions are usually defined according to obvious temperature differences, while in tropical and sub-tropical areas, where mean monthly temperatures are more equable, season are often based on the level of recorded or expected precipitation. Due to the variability in monthly rainfall at Weza (Fig. 2.3), the main climatological parameters incorporated in the definition of seasons in this study were mean monthly maximum and minimum temperatures. Unless otherwise stated, references to seasons throughout this study fall within the categories summarised in Table 2.3.

TABLE 2.3 Climatic definition of seasons at Weza

Season	Months	Mean max. temp.(°C)	Mean min. temp.(°C)	% of mean annual rainfall
Summer	Dec Jan Feb	> 25	> 16	43%
Autumn	Mar Apr May	< 25 > 20	< 16 > 9	23%
Winter	Jun Jul Aug	< 20	< 8	6%
Spring	Sep Oct Nov	> 20 < 24	> 9 < 14	28%

2.6 LAND USE AND MANAGEMENT

The Weza State Forest is managed on a multiple use basis. Three main vegetation classes are present and managed according to their needs and uses.

2.6.1 Mountain Grassland

Mountain grasslands form approximately 27% of the total area at Weza and occur mainly along the Ingeli Range (Fig. 2.6), where the high rainfall and cold climate, shallow soils and steep and rocky slopes constitute an unsuitable area for tree growth. Conservation management principles are applied to these slopes for the production of clear silt-free water. However, due to the serious threat of wildfires originating from the Transkei beyond the western boundary, it has been found necessary to burn this grassland in autumn rather than after the first spring rains, as occurs in other Forestry water catchment areas (J.T. Nel, pers. comm.).

The area is divided into a number of blocks, the boundaries of which are cleared of vegetation by the application of a herbicide. This ensures that burning is confined to scheduled alternate blocks, which are burnt every second year, and at a times when damage to grass roots would be minimal.

Project objectives and the relative densities of bushbuck and duiker in the region precluded the inclusion of mountain grasslands within the extensive or intensive study areas.

2.6.2 Indigenous Forests

Several extensive and numerous smaller indigenous forests cover approximately 19% of the total area at Weza

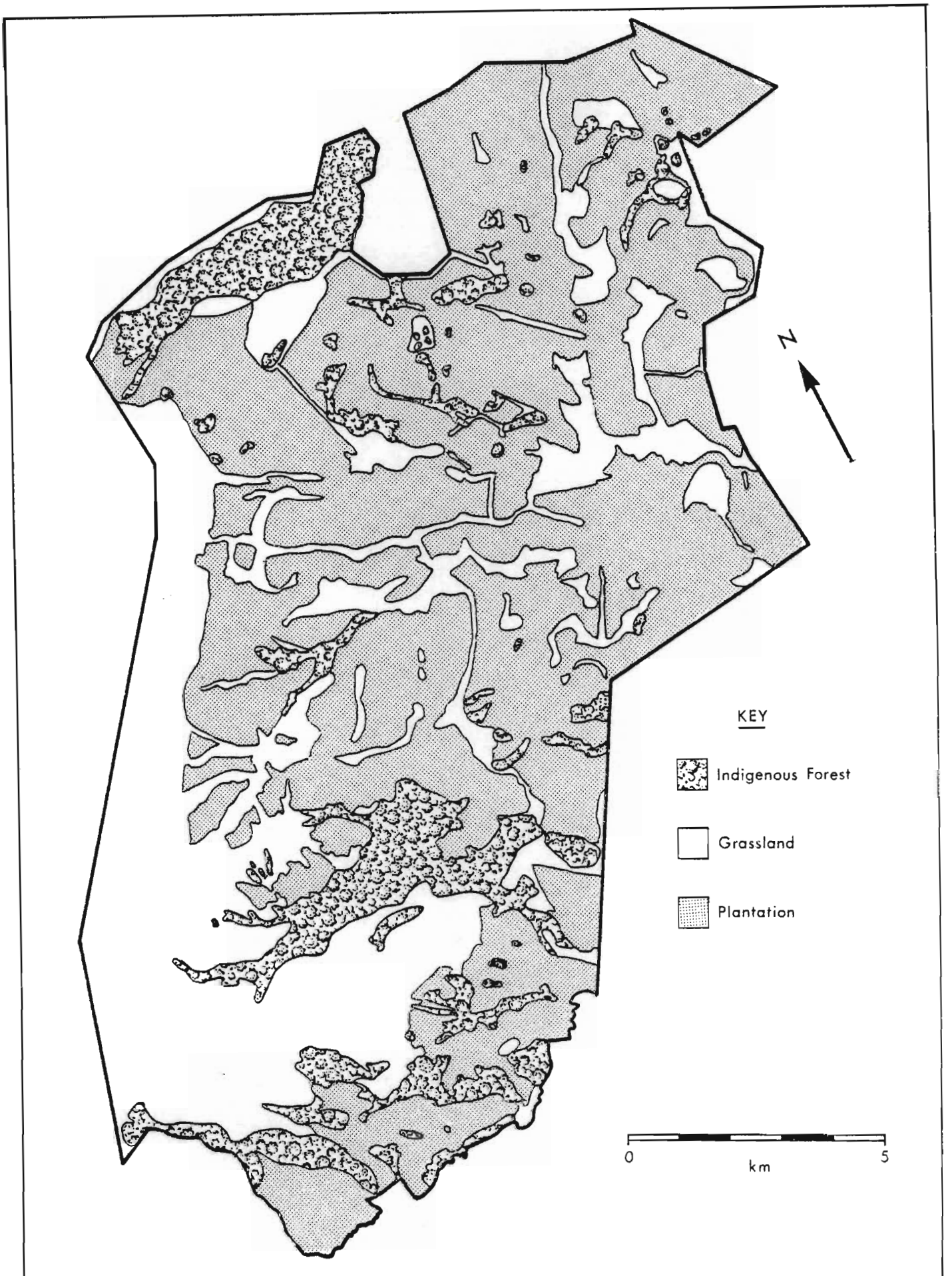


FIGURE 2.6 The major vegetation communities in Weza State Forest.

State Forest. These are largely confined to the moist cooler south facing slopes (Fig. 2.6), and apart from the limited exploitation of dead or damaged trees, have been totally protected for the last 45 years. Prior to this the forests were heavily exploited for their timber, particularly yellowwoods and stinkwoods.

Although the forests are protected as nature reserves, trees are still damaged when Zulus and Xhosas illegally strip the bark from certain species (particularly stinkwood and assegai (Curtisia dentata)) for medicinal purposes. Management of these forests also includes the control of invading alien species, particularly Mauritius thorn (Caesalpinea decapetala), bugweed (Solanum mauritianum) and wattles (Acacia spp.) and the control of snares and other forms of poaching. Indigenous forests were included in both the extensive and intensive study areas.

2.6.3 Plantations

Approximately 50% (10 989 ha) of the total area of Weza State Forest is covered by plantations (Fig. 2.6), while a further 4% is suitable for afforestation and will be planted in due course. These plantations are managed much more intensively than either grasslands or indigenous forests, and in keeping with the objectives of this study (Chapter One), constituted the dominant vegetation community in both the extensive and intensive study areas (see below). A sound knowledge of the extent, duration and intensity of silvicultural and exploitation activities is required before any assessment can be made of the impact such practices have on animal movements, feeding strategies and habitat utilization and selection. Consequently, the following account of plantation management is necessarily rather detailed while the influences that these practices and resultant habitat modifications have on animals distributions and population performance are considered in Chapter Six to Chapter Ten.

The main management objective of the plantations is to produce a sustained yield of high quality veneer logs and softwood saw timber on a thirty year rotation. The major softwood species currently grown and Weza are Pinus elliottii (slash pine), P. patula (patula pine) and P. taeda (loblolly pine) which together constitute 85% of the total plantation. Areas covered by these and other species are shown in Table 2.4.

Many of these other species were frequently planted at Weza in the past, but proved to be unsuitable and are gradually being replaced by one of the three main pine species. This is particularly true of the Eucalyptus spp. which were originally planted in narrow strips as fire belts, but were found to be ineffective. Since gum seedlings readily invade pine stands, these belts are rapidly being felled, and depending on the quality and size, the timber is sold and used for veneer, furniture, joinery, mining timber or pulpwood used in the manufacture of insulation boards and rayon. Wattles and blackwood (Acacia melanoxylon) are also regarded as invasive weeds at Weza and Acacia spp. are no longer planted. Stands of mature trees are harvested and auctioned or sold as firewood. The importance of poplar (Populus deltoides) which is largely used in the match and shoe industries, has fluctuated according to demand and market prices, but at present this species occupies less than 1% of the total plantation area.

The vast majority of timber produced at Weza is softwood and approximately 104 000 m^3 of veneer and sawlog timber are sold annually for industrial and structural use. Softwood pulp accounts for a further 40 000 m^3, while 12 000 m^3 of Eucalyptus pulp, 2 600 m^3 of poplar and 6 000 m^3 from other species (mainly for use as firewood) are produced per annum (J.T. Nel, pers. comm.). At a current price of R24,00/m^3 for logs felled and stacked in the field (P. Fifield, pers. comm.), the annual production of 104 000 m^3 of sawlog timber alone represents a gross income in excess of R2,5 million per annum.

TABLE 2.4 Area of plantation utilization (ha) by age class and species, at Weza State Forest, 1982.

Species	Age class (yrs)						Total area	Species as % of total plantation
	0-2	3-12	13-22	23-32	33+	Unclas-sified		
Pinus elliottii	657,2	1 685,9	463,6	264,1	26,8	0,0	3 097,6	28.2%
Pinus patula	62,4	458,6	1 620,6	1 726,1	178,0	19,0	4 064,7	37,0%
Pinus taeda	227,3	1 464,0	457,2	0,0	10,8	0,0	2 159,3	19,6%
Pinus roxburghii	0,0	24,0	0,0	0,0	143,7	0,0	167,7	1,5%
Other pine species	0,0	10,7	28,7	127,4	202,2	0,0	368,8	3,4%
Cupressus species	0,0	0,0	0,0	0,0	36,0	0,0	36,0	0,3%
Cryptomeria japonica	0,0	3,7	20,6	0,0	15,4	0,0	39,7	0,4%
Other softwoods	0,0	3,0	0,0	0,0	0,3	0,0	30,3	0,0%
Subtotal softwoods	946,9	3 649,9	2 590,7	2 117,6	613,0	19,0	9 937,1	90,4%
Eucalyptus species	0,0	7,8	177,9	0,0	93,3	0,0	279,0	2,5%
Populus deltoides	19,5	10,9	53,5	7,7	2,2	0,0	93,8	0,9%
Acacia melanoxylon	0,0	1,2	0,0	0,0	86,3	0,0	87,5	0,8%
Other hardwoods	1,2	19,8	77,0	0,0	8,5	4,6	111,1	1,0%
Subtotal hardwoods	20,7	39,7	308,4	7,7	190,3	4,6	571,4	5,2%
Arboreta	0,0	3,0	0,0	0,0	0,0	9,7	12,7	0,1%
Temporary unplanted areas	0,0	0,0	0,0	0,0	0,0	467,7	467,7	4,3%
Total	967,6	3 692,6	2 889,1	2 125,3	803,3	501,1	10 988,9	100,0%
Age class as % of the total area	8,8%	33,6%	26,4%	19,3%	7,3%	4,6%	100,0%	

Exploitation of other plantation products includes the removal of firewood (usually the trash resulting from uneconomic thinnings, etc.), by hand at a nominal fee, and the harvesting of the mushroom Boletus edulis by a private concern. These mushrooms grow during October to April under mature stands of P. patula and P. taeda and are particularly prolific at higher altitudes. They are picked by hand, cleaned, sliced and dried and exported to Europe. Over

11 000 kg of fresh Boletus have been harvested since exploitation started in 1982, and these mushrooms have generated an income exceeding R4 500 to the Directorate of Forestry to date (A. Zunkel, pers. comm.).

As in the indigenous forest, all forms of wildlife within the plantation are protected, and the area is regularly patrolled to prevent illegal activities such as grazing by neighbouring livestock, unauthorised entry and poaching.

Weza plantation is currently divided into 19 separate management blocks. All of these are subdivided into numerous compartments, each compartment being a temporal management unit. Compartments vary in size according to topography, natural and artificial boundaries, timber species requirements, availability of space, etc., and may be amalgamated or subdivided as local management decisions alter. A total of 1 063 compartments, with an average area of 10,3 ha, were registered at Weza in 1982 (unpublished Forestry records). Since each compartment may differ considerably from those surrounding it in terms of timber species, composition and age, area and management history, the compartments form a mosaic of extremely heterogeneous habitats (Plate 1). This diversity is further compounded by the numerous management practices that are implemented annually in certain areas of the plantation, or that are prescribed according to the age and growth of the timber species growing within each compartment, as outlined below.

2.6.3.1 Fire protection

Firebreaks are prepared annually at Weza during May, June and July. These belts are at least 20 m wide on the boundary of the plantation and are prepared by either burning (after the first frosts), by mechanical means (ploughing and hoeing) or by the use of herbicides. Wide fire belts are also prepared internally, and these together with natural boundaries separate the area into the nineteen management blocks. Internal firebreaks, or "cut-outs" may be burnt

PLATE 1. Aerial photograph of Intensive Study Area 1 in June 1983 (Scale 1:12 000).

every one or two years, depending on their importance as grazing areas for Forestry livestock. The plantation is further segmented by the clearing of all vegetation within 3 m of each side of the major internal roads. Four fire towers are continually staffed during the fire season (June to October) and fires are located by triangulation.

2.6.3.2 Silviculture

2.6.3.2.1 Afforestation and reforestation

Young trees are raised from improved seed at the Weza nursery, and are usually planted out when 15-20 cm tall. The compartment to be planted is prepared firstly by marking the site where each seedling is to be planted ("lining out"), and then by clearing and digging each site ("pitting"). Cleared pits vary in size according to the extent of grass and weed growth in the compartment, but are commonly one metre in diameter. Seedlings are then planted at a spacing of 2,7 m x 2,7 m, i.e. at a density of 1370/ha. Compartments with seedlings are usually weeded or "cleaned", at least annually, and usually before spring, for three years until the young trees are firmly established. If the mortality rate of the seedlings exceeds 10% then they are replaced ("blanking") usually during the following year.

2.6.3.2.2 Thinning

Although pine seedlings are planted out a density of 1370/ha, only 18% of these are maintained and harvested as mature timber. The remaining trees are felled during three density reduction programmes or "thinnings". Marsh (1978) lists three main reasons for thinning, namely to concentrate the increment on the best-formed trees by removing the defective ones, to renew growth by reducing over-crowding in the stand, and to ensure that the renewed growth takes place under uniform conditions of light and spacing. The thinning regime currently employed at Weza is summarised in Table 2.5. Poplars are not thinned at Weza and have a planting esplacement of 3,7 m and a harvesting rotation of 20 years.

TABLE 2.5 Pine thinning regime at Weza State Forest.

Age when thinned (yrs)	Density after thinning (stems/ha)	Use of felled trees
8	650	Uneconomic, remain as slash
13	400	Pulp (and possibly some saw timber)
18	250	Saw timber and pulp (tops)
30	0	Saw timber and pulp (tops)

2.6.3.2.3 Pruning

Unlike Eucalyptus spp., the pines grown at Weza have no mechanism for shedding dead branches. Consequently these limbs may remain attached to the stem for many years and by the time they rot and fall off, dead or loose knots have formed. Since knots reduce the strength and quality of sawlog timber, (and may not exceed a diameter of 90 mm in the Directorate of Forestry's specifications for softwood sawlogs; Marsh 1978), the problems of knot formation is solved by pruning live branches. These are removed at regular intervals up to a height of 7 m from the ground, (this section of the stem contains a large proportion of the usable timber and yields the largest diameter and most valuable logs). The timing of the pruning is determined by the height of the dominant trees within each compartment and is summarised in Table 2.6. Pruning is always completed before the second thinning occurs.

2.6.3.3 Harvesting

Once trees are felled by chain saw, they are debranched and cut to standard log lengths. The final crop of trees are removed at one time (clearfelling) rather than in stages, and the slash is not burnt, but heaped into rows and left to

TABLE 2.6 Pine pruning regime at Weza State Forest.

Height of dominant tree (m)	Approximate age (yrs)	Height pruned (m)
3,5 m	4-5	0-1,5 *
6 m	6-7	0-3
9 m	8-10	0-5
12 m	10-12	0-7

* P. patula only

decompose. Every attempt is made to reforest the compartment within the same year, to prevent competition with the pioneer species of weeds.

The logs are dragged ("slipped") to the roadside by either mules (small logs from thinnings) or by tractors and skidders. Here they are graded according to length and diameter measurements, (the minimum diameter for saw logs being 19 cm), and then loaded onto large vehicles by means of mobile cranes or self-loading lorries.

2.6.3.4 Weed control

Weed problems increase dramatically with the start of the second rotation, and consequently weed growth is controlled, usually before the weeds seed, for the first three years after reforestation. Afforested areas usually require less attention and cleaning, where necessary, is confined to the pit site. Thereafter weeds are usually treated in conjunction with other silvicultural practices (e.g.. prior to all prunings and most thinnings), but compartments with particularly vigorous stands of invasive wattles and gums may be cleaned periodically.

Although dense weed growth increases the mortality rate of young trees and suppresses their growth, causes crooked stems, obstructs silvicultural operations and hinders firefighting efforts, (Marsh 1978), weeds are extremely

common at Weza. Due to financial constraints, weedkillers are only utilized in the removal of Eucalyptus stumps and in the construction of narrow fire belts adjacent to some major roads. The major form of control is slashing, even though this practice offers only temporary relief and often results in the coppicing of certain species (e.g. bugweed). The most dominant weed species at Weza include bramble (Rubus spp.), bugweed, wattles and blackwood, eucalypts, and regenerating pines.

2.6.3.5 Control of damage caused to commercial species.

The greatest potential hazard to plantations is fire, and methods employed to prevent or control forest fires have already been described.

Attempts to control damage caused by wildlife (mainly rodents, antelope and to a much lesser extent baboons) include the use of repellants and the temporary erection of electric fences (discussed further in Chapters Six and Seven). No practical control methods exist for the protection of pines against climatic agencies except in the selection of the most suitable species for the prevailing conditions. Patula pines are more susceptible than slash or loblolly pines to damage caused by wind or hail, and to infection by the fungus Diplodia pinea after hail damage (Marsh 1978). As a result, more areas of Weza were planted with P.elliottii and P.taeda in the late 1970's. However, more recently, the quality of the timber produced from P. taeda has declined due to the species' reaction (tapered stems and distortion) to infestations of the black aphid (Cinara cronartii), and loblolly pines have not been planted during the last two years (J.T. Nel, pers.comm.). Since a monoculture is undesirable at Weza, it is unlikely that P. elliottii alone will be planted, particularly since this species tends to form pockets of resin within the timber, thus decreasing its economic value. P. patula will probably again become a major species, despite its limitations, and the choice of timber species grown at Weza will continue to be based on a number of environmental and economic factors.

Although damage is occasionally caused to the foliage and bark of all pine species by various insects (e.g. Hylastes augustatus, Eulachnus rileyi and Possodes nemorensis), attacks have not been so virulent as to necessitate control measures to date.

2.6.3.6 Construction of roads

With over 800 km of established roads and numerous tracks, the majority of the plantation is extremely accessible (Fig. 2.7) and new roads or tracks are only constructed to facilitate harvesting or afforestation operations. Consequently, they are not routed through indigenous forests but are confined to the plantation and open grassland.

2.6.4 Recreation

In keeping with the Directorate of Forestry's multiple land use policy, several recreational facilities are available at Weza, including picnic sites, hiking and educational trails, and trout fishing.

The Ngele Hiking Trail offers a choice of several routes (all clearly marked in the field and on a comprehensive map), varying from 30 km to 50 km through all of the major vegetation types. Overnight accommodation for a maximum of thirty individuals, is provided in converted farmhouses with ablution facilities, basic furniture, firewood etc., at each of the four sections of the trail, and at a cost of R4,00 per adult (R2,50 per scholar or R1,00 each for parties of school children). The Ngele trail which is not open during the fire season of July to September inclusive, is administered by the National Hiking Way Board, and is one of two trails currently available offering the above amenities on State land in Natal.

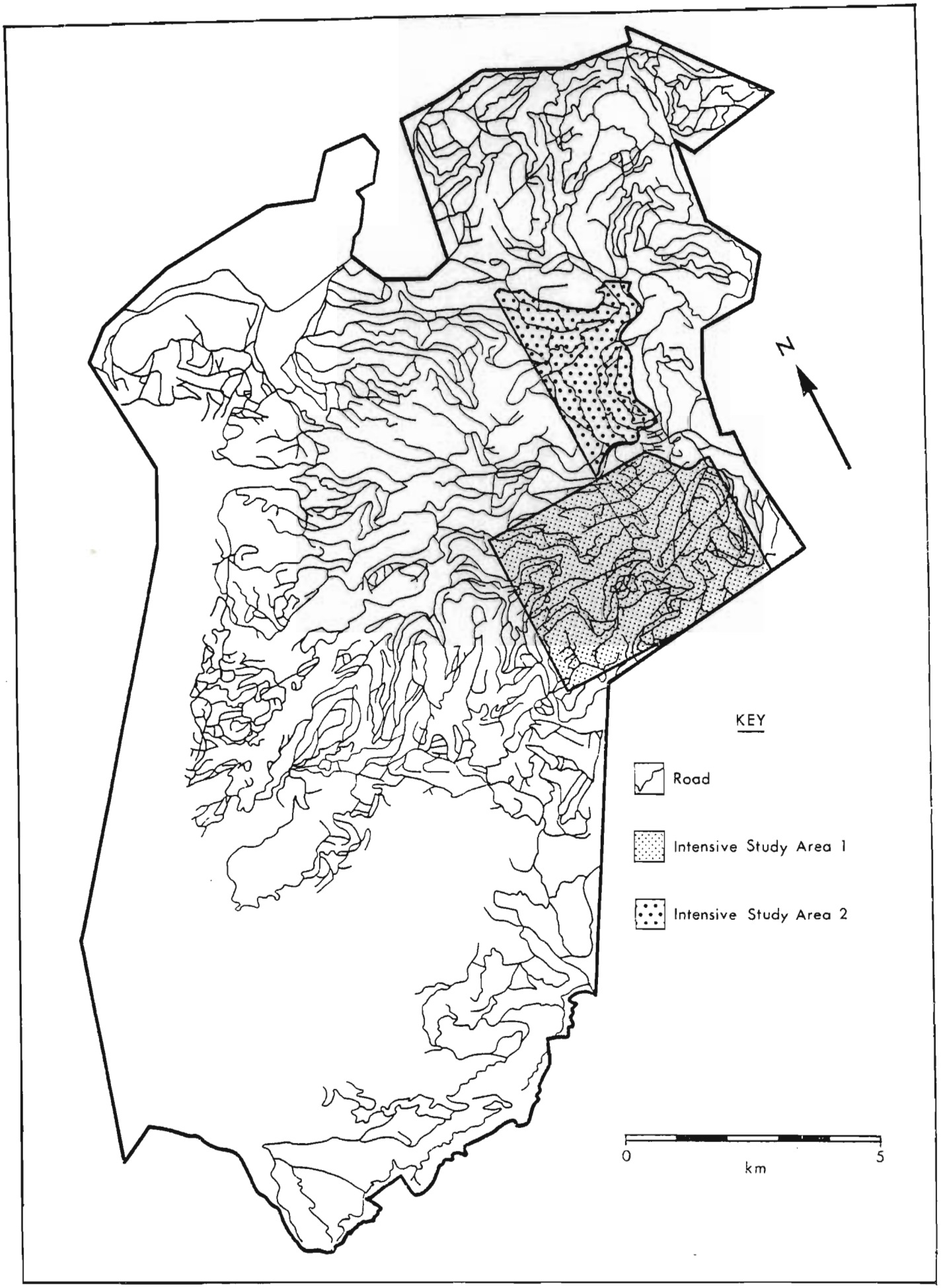


FIGURE 2.7 The network of roads and location of the two intensive study areas in Weza State Forest.

Overnight accommodation and short self-guided educational trails are also offered at the Lorna Doone Forest Hostel, which is specifically designed for school and youth groups. The hostel can accommodate a maximum of forty individuals in conditions similar to those offered on the Ngele Trail, but at a reduced tariff, and informative leaflets concerning the history, management and wildlife of the area are available.

River fishing for rainbow trout (Salmo gairdneri) is offered during the open season (1st September to 1st June) each year at a cost of R4,00 per season or 50c per day. Two dams have also been stocked with trout, one of which provides all-year fishing, and a daily charge of R1,00 per rod is levied for fishing these waters. All anglers must be in possession of a valid trout licence (R3,00 per annum) and the regulations enforced on scheduled trout waters elsewhere are also applicable at Weza.

2.7 VEGETATION

Three natural veld types occur at Weza, namely the Ngongoni Veld, the Dohne Sourveld and the Highland Sourveld (Acocks 1975).

2.7.1 Grassland

The Ngongoni Veld occurs at lower altitudes than either Dohne or Highland Sourvelds and is thus largely confined to the eastern section of Weza. Where the forests of this vegetation type have disappeared, they have been replaced with a very open thornveld that is dominated by the grasses Themeda triandra or more commonly, Aristida junciformis.

The Dohne Sourveld occurs up to 1 300 m above sea level and thus occupies the central portion of Weza State Forest,

while the Highland Sourveld which occurs at altitudes above 1 300 m, is confined largely to the western mountain range and the higher ridges. Where the forests are replaced, both Dohne and Highland Sourvelds become dense grassvelds and the latter on parts of the mountain slopes tends towards Protea Savanna (Acocks 1975).

While the grasslands of these three veld types are less contiguous than their forest counterparts, (largely as a result of plantation management), they share many of the same common species including Themeda triandra, Monocybium ceresiiformes, Hyparrhenia hirta, Eragrostis capensis, Heteropogon contortus, Aristidia junciformis and Cymbopogon validus (Acocks 1975; A. Nicholas, pers. comm.). Dominant families in the area include Asteraceae, Cyperaceae, Leguminosae, Liliaceae and Poaceae, while members of the Asclepiadaceae, Crassulaceae, Hypoxidaceae, Iridaceae, Laminaceae, Orchidaceae, Periplocaceae, Polygalaceae, Scrophulariaceae, and Thymelaeaceae are also common (A. Nicholas, pers. comm.).

2.7.2 Forests

Representative species from all three veld types occur in each of the several large indigenous forests at Weza and the more common species of trees are listed in Appendix A .

As with grasslands, species diversity tends to be greatest at the lower altitudes (Ngongoni veld) where the dominant species are Combretum Krausii, Trimeria grandifolia, Cryptocarya woodii, Rapanea melanophloeos and Xymalos monospora. Podocarpus falcatus and P. latifolius become the dominant trees in the Dohne sourveld forests, while P. latifolius and Leucosidea sericea are dominant in the Mountain sourveld, the latter species particularly at forest margins and at the upper limits.

Common small trees and shrubs in the understory of these forests include Allophylus decipiens, Buddlea salviifolia, Canthium spp., Calpurnia aurea, Carissa bispinosa, Clausena anisata, Diospyros spp., Eugenia zuluensis, Grewia occidentialis, Myrsine africana, and Scutia myrtina as well as saplings of many of the larger trees in Appendix A.1 .

Numerous forbs, grasses, ferns and climbing species also occur in the understory, examples being Protosparagus spp., Blechnum attenuatum, Begonia sutherlandii, Hypoestes spp. Impatiens dutheiae, Isoglossa spp., Oplismenus hirtellus, and Plectranthus spp.

2.7.3 Plantations

Afforestation has rarely been accomplished at heights exceeding 1 400 m above sea level at Weza and consequently the Mountain Sourveld has largely been unaffected by exotic timber production. Although the plantations are predominated by Pinus spp., numerous other exotics were planted for commercial or research purposes in the past, and many of these remain in discrete patches today (Appendix A.2).

Several other exotic species have become established at Weza, particularly in the gardens of old homestead and on old agricultural land, and include lemon and orange trees (Citrus limon and C. aurantium), peach (Prunus persica), mulberry (Morus alba), privets (Ligustrum spp.), cotoneaster (Cotoneaster spp.), figs (Ficus carica) and Mexican hawthorns (Crataegus pubescens). Confined areas adjacent to plantations have also been cultivated for the production of agricultural crops (e.g. maize, cabbages and potatoes) for labour consumption and to provide fodder (e.g. Eragrostis spp.) for Forestry livestock.

The seedlings of several commercial species have invaded many areas of Weza and there are numerous blackwood, wattles

and gum thickets. These exotics also predominate the understories of many pine compartments which also include bramble, bugweed, goat's apple (Solanum aculeastrum), wild gooseberry (Physalis peruviana), blackjack (Bidens biternata), khaki bush (Tagetes minuta), inkberry (Phytolacca heptandra), Pellaea viridis, Protoasparagus spp., Senecio spp., Pteridium aquilinum and regenerating pine species. The majority of these species are also pioneers of clearfelled areas.

Much of the indigenous vegetation was removed before the mandatory practice of retaining a natural 20 m belt along all river courses (and indigenous forest) was implemented at Weza, and as a result of this action, silver, green, golden and black wattles (Acacia dealbata, A. decurrens, A. longifolia and A. mearnsii respectively), blackwoods, and bugweed are now firmly established along many of the water courses traversing the plantations.

2.8 FAUNA

In the absence of any research input, the wildlife at Weza has, for the last 30 years or so, been managed by the Directorate of Forestry on a policy of total preservation. Prior to this, limited sport hunting of bushbuck, grey duiker and blue duiker was permitted for several years at arbitrary levels of exploitation (F. Raw, pers. comm.). Species, numbers, abundance and distribution have thus largely been ignored, or at best assessed subjectively, and no attention has been given to the trends or changes of any population.

2.8.1 Mammals

Bushbuck are numerous throughout Weza State Forest and constitute the largest herbivore biomass. Grey duiker are slightly less numerous in the plantations and avoid the indigenous forest, but unlike bushbuck may permanently inhabit grassland areas. Other unguiates include grey

rhebuck (Pelea capreolus), and oribi (Ourebia ourebi), both of which are fairly common on the Highland Sourveld, with the latter species more often encountered in the lower slopes and bordering afforested areas. Both of these antelope may descend to some of the adjacent cut-outs during the winter months. Blue duiker were common in the indigenous forest in the past (F. Raw, pers. comm.), but have not been seen for the last six years. Ten individuals were re-introduced at Weza by the author in 1982 but their present status is not known. Although low numbers of reedbuck (Redunca arundinum) occur on neighbouring farms, these are absent, or at best extremely scarce at Weza.

The lynx (Felis caracal) is the largest natural predator at Weza and occurs throughout the area at low densities. Black-backed jackal (Canis mesomelas) are seldom seen or heard, and must be considered as rare. The most common and widely distributed small carnivore is the large spotted genet (Genetta tigrina), while the large grey mongoose (Herpestes ichneumon), the slender mongoose (H. sanguineus), the white-tailed mongoose (Ichneumia albicauda) and the marsh mongoose (Atilax paludinosus) are largely confined to grassland and riverine areas and settlements. Unlike the large spotted genet, none of these mongooses are encountered in the plantations.

Other small carnivores include the African wild cat (Felis libyca) and the feral cat (F. catus), both of which are widely distributed and common, and the striped polecat (Ictonyx striatus) which is rare. Unknown numbers of otters, probably the cape clawless otter (Aonyx capensis) but possibly the spotted-necked otter (Lutra maculicollis) occur in the numerous rivers and streams at Weza.

Baboons (Papio ursinus) are common throughout the plantations while the indigenous forests support both vervet and samango monkeys (Cercopithicus aethiops pygerythrus and C. albogularis respectively), the latter species being more numerous.

Reasonable numbers of rock hyrax (Procavia capensis) are confined to the rocky outcrops and ridges at the cut-outs, and antbears (Orycteropus afer) are occasionally encountered in open grassland, where hares, probably cape and/or scrub hares (Lepus capensis/L.saxatilis) are also fairly common. The red rock hare (Pronolagus crassicaudatus) also occurs at Weza and is usually found on rocky cut-outs or occasionally in clearfelled areas.

Several species of rodents are common, the largest being the porcupine (Hystrix africae-australis) which occurs throughout the Forest. Other species include the cane rat (Thyronomys swinderianus) which is confined to reedbeds and dense grassland, the vlei rat (Otomys irroratus), the four-striped field mouse (Rhabdomys pumilio), and the pygmy mouse (Mus minutoides). Additional rodents must occur in the area, but, like the insectivores, specimens have not been available for identification. Details of other vertebrate species encountered at Weza during the course of this study will be published elsewhere (Allen-Rowlandson and Raw, in prep).

2.9 INTENSIVE STUDY AREAS

Two areas were selected for intensive studies of bushbuck and duiker abundance, social and spatial organisation, habitat preferences and responses to management activities. Reasons for selecting these regions (shown on Fig. 2.7) included the relatively high densities of undisturbed bushbuck and representative vegetation in the first area (Intensive Study Area 1) and the common occurrence of duiker in an area scheduled to receive a high degree of timber management activities in the second area (Intensive Study Area 2). To a lesser extent the areas were also chosen to facilitate field observations, radio telemetry and travel.

2.9.1 Intensive Study Area 1 (I.S.A.1)

This area, which represented 7,4% of Weza State Forest, contained 1 400 ha of plantations (12,7% of total plantation area) and 200 ha of grassland, indigenous forest and thickets (Fig. 2.8). The age structure and species composition of the plantation within I.S.A.1 (Table 2.7) closely resembled the entire plantation area (Table 2.4) in 1982. The average size of the 200 compartments occurring in this area was 7,0 ha.

TABLE 2.7 Area of plantation utilization (ha) by age class and species, at Intensive Study Area 1, 1982.

Species	Age class (yrs)						Total area	Species as % of total Study area
	0-2	3-12	13-22	23-32	33+	Unclas-sified		
Pinus elliottii	6,7	133,4	104,5	0,0	0,0	0,0	244,6	17,5%
Pinus patula	0,0	27,6	219,5	124,7	10,8	0,0	382,6	27,3%
Pinus taeda	68,4	219,3	198,7	0,0	0,0	4,1	490,5	35,0%
Pinus roxburghii	0,0	0,0	0,0	0,0	0,0	1,6	1,6	0,1%
Other pine species	0,0	0,0	0,0	0,0	81,3	0,7	82,0	5,9%
Cupressus species	0,0	0,0	0,0	0,0	0,0	5,9	5,9	0,4%
Other softwoods	0,0	0,0	0,0	0,0	0,0	0,3	0,3	0,0%
Subtotal softwoods	75,1	380,3	522,7	124,7	92,1	12,6	1 207,5	86,2%
Eucalyptus species	0,0	0,0	1,6	0,0	2,6	27,5	31,7	2,2%
Populus deltoides	10,0	7,2	23,9	7,7	0,0	1,0	49,8	3,5%
Acacia melanoxylon	0,0	0,0	0,0	0,0	0,0	3,7	3,7	0,3%
Other hardwoods	9,1	0,0	0,1	0,0	0,0	3,4	12,6	0,9%
Subtotal hardwoods	19,1	7,2	25,6	7,7	2,6	35,6	97,8	6,9%
Arboreta	0,0	2,2	0,0	0,0	0,0	0,0	2,2	0,2%
Temporary unplanted areas	0,0	0,0	0,0	0,0	0,0	93,4	93,4	6,7%
Total	**94,2**	**389,7**	**548,3**	**132,4**	**94,7**	**141,6**	**1 400,9**	**100,0%**
Age class as % of the total area	6,7%	27,8%	39,1%	9,5%	6,8%	10,1%	100,0%	

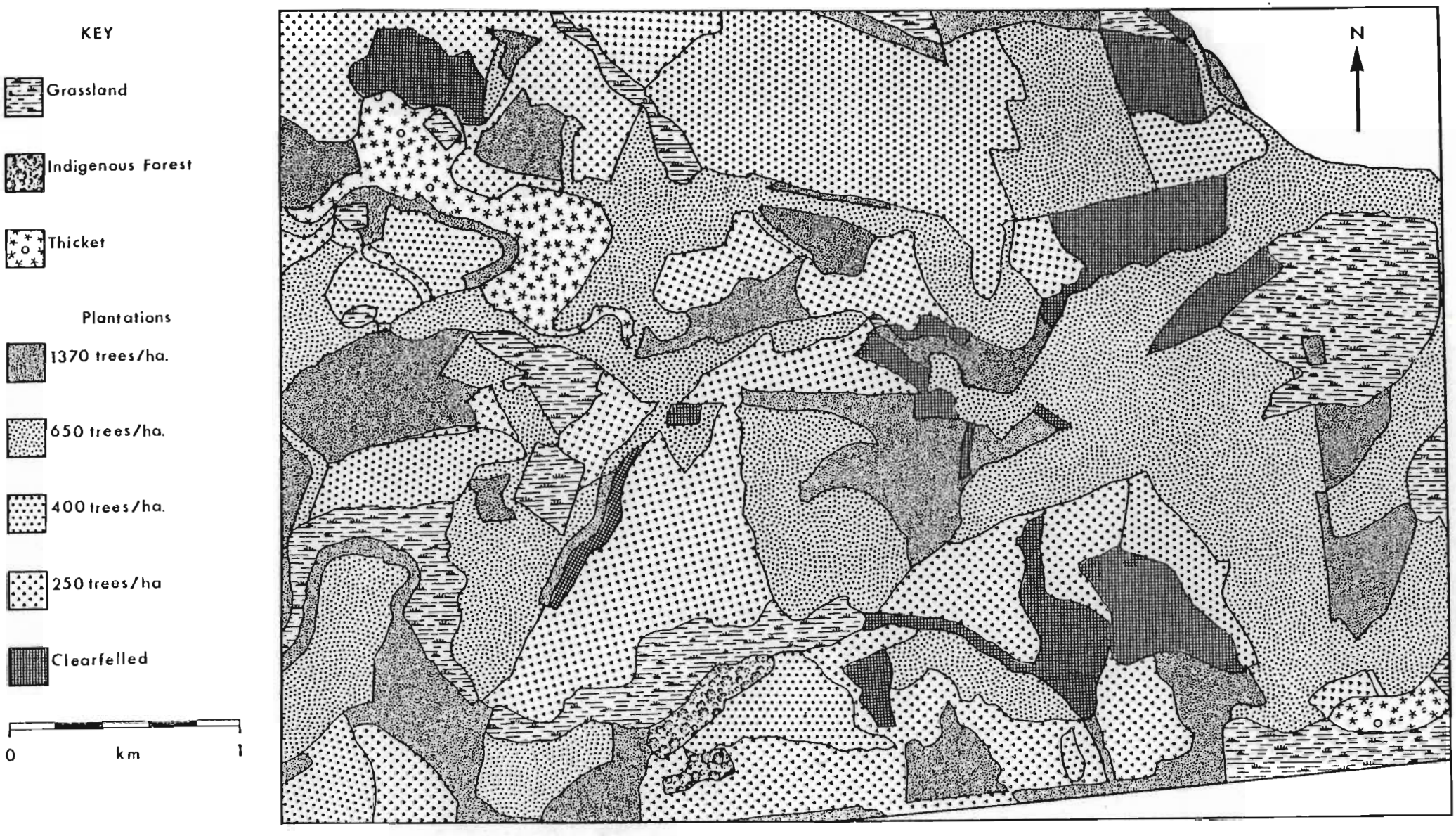


FIGURE 2.8 The major vegetation communities and densities of exotic trees in Intensive Study Area 1 during 1982.

2.9.2 Intensive Study Area 2 (I.S.A.2)

This region was approximately half the size of I.S.A.1, totalling 739 ha (3,4% of Weza State Forest) and consisted almost entirely of plantations and temporary unplanted ground (Fig. 2.9). Compared to the entire plantation (Table 2.4) this area had notably fewer hardwoods and a much higher proportion of young trees (Table 2.8). The 43 compartments forming this area were considerably larger than those in I.S.A.1, with an average size of 17,0 ha.

TABLE 2.8 Area of plantation utilization (ha) by age class and species at Intensive Study Area 2, 1982.

Species	Age class (yrs)						Total area	Species as % of total Study area
	0-2	3-12	13-22	23-32	33+	Unclas-sified		
Pinus elliottii	26,0	139,9	49,6	56,5	0,0	0,0	272,0	36,8%
Pinus patula	0,0	30,5	27,8	55,4	0,0	0,0	113,7	15,4%
Pinus taeda	52,4	206,9	0,0	0,0	0,0	0,0	259,3	35,1%
Pinus roxburghii	0,0	24,0	0,0	0,0	0,0	0,0	24,0	3,2%
Subtotal softwoods	78,4	401,3	77,4	111,9	0,0	0,0	669,0	90,6%
Populus deltoides	0,0	0,0	27,1	0,0	0,0	0,0	27,1	3,7%
Arboreta	0,0	2,7	0,0	0,0	0,0	0,4	3,1	0,4%
Temporary unplanted areas	0,0	0,0	0,0	0,0	0,0	39,5	39,5	5,3%
Total	**78,4**	**404,5**	**104,5**	**111,9**	**0,0**	**39,9**	**738,7**	**100,0%**
Age class as % of the total area	10,6%	54,7%	14,1%	15,1%	0,0%	5,4%	100,0%	

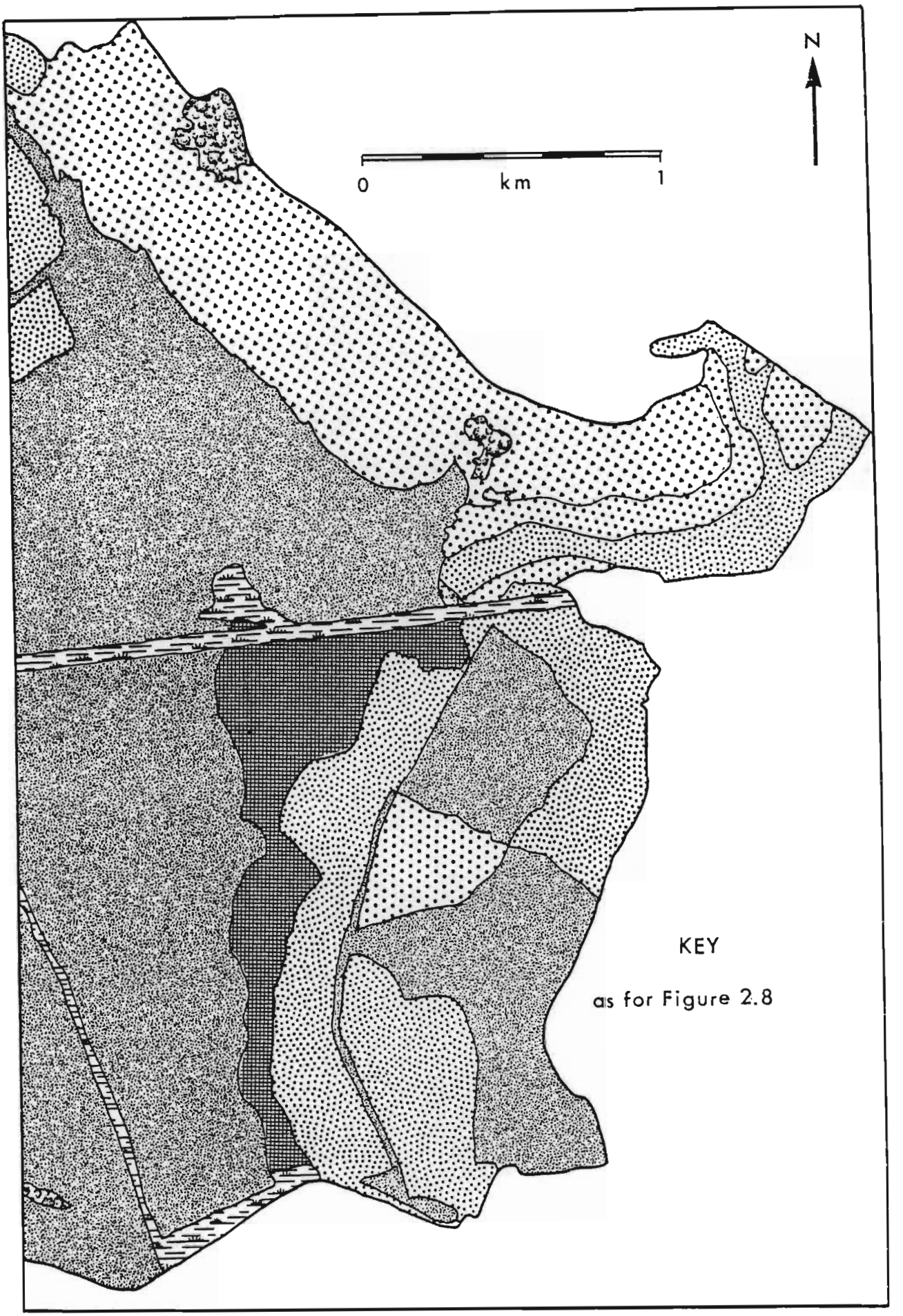


FIGURE 2.9 The major vegetation communities and densities of exotic trees in Intensive Study Area 2 during 1982.

2.9.3 Management Activities

The proportions of each study area receiving one of several timber management activities every year from 1980 to 1984 are summarised in Table 2.9, while the cumulative areas of activity at I.S.A.1 and I.S.A.2 during 1980 to 1984 were 75,3% and 79,5% respectively. The effects (including duration and extent) of these on the performance of both the bushbuck and duiker populations are considered in Chapter Ten.

TABLE 2.9 The proportions (%) of the extensive study area (E) Intensive Study Area 1 (I.S.A.1) and Intensive Study Area 2 (I.S.A.2) directly influenced by management activities each year from 1980 to 1984.

Activity	1980-1981			1981-1982			1982-1983			1983-1984		
	E	ISA1	ISA2	E	ISA1	ISA2	E	ISA1	ISA2	E	ISA1	ISA2
Clearfelling	N/A	0,4	0,0	3,3	5,7	0,0	2,9	4,4	0,0	3,4	3,4	6,8
3rd thinning	N/A	0,8	0,0	1,7	2,5	0,0	0,8	0,0	0,0	2,1	6,9	0,0
2nd thinning	N/A	0,0	0,0	3,5	4,3	5,0	4,1	10,3	5,4	4,1	9,6	0,0
1st thinning	N/A	2,2	0,0	2,2	3,3	0,0	4,6	3,5	16,9	4,8	5,7	16,3
Subtotal thinning	N/A	3,0	0,0	7,4	10,1	5,0	9,5	13,8	22,3	11,0	22,2	11,3
Pruning	N/A	6,4	33,7	15,0	21,6	14,6	8,8	6,0	25,2	10,4	12,9	16,1
Cleaning/slashing	N/A	12,3	43,9	27,6	29,4	23,6	10,3	10,2	19,7	17,6	24,5	17,9
Reforestation	N/A	0,0	0,0	2,7	1,1	0,0	2,5	6,3	0,0	3,6	3,7	5,8
Afforestation	N/A	1,4	0,0	0,0	0,0	5,7	0,0	0,0	5,1	0,0	0,0	0,0
Total of area	**N/A**	**23,5**	**77,6**	**56,0**	**64,4**	**48,9**	**34,0**	**40,7**	**73,3**	**46,0**	**66,4**	**56,0**

CHAPTER THREE
AGE DETERMINATION AND GROWTH

3.1 INTRODUCTION

The ability to determine the ages of individual animals is an essential prerequisite for many wildlife population studies. Although the degree of precision required in estimating individual ages depends largely on specific objectives, techniques that facilitate age estimation at the practical level are often sufficient for management purposes (Keiss 1969;Spinage 1973a; Thomas and Bandy 1975; Mitchell et al. 1977). Higher levels of accuracy are invariably required for growth and population dynamics studies (Erickson et al. 1970; Kerwin and Mitchell 1971; Hanks 1972a), particularly when age-specific events in the lives of individuals within a population are being examined. Such relevant events include the attainment of physical, sexual and social maturity, reproductive performance and decline, and longevity (Spinage 1973a). Accurate determination of age is also required for comparing the growth, breeding performance and survival of individuals from different populations (Mitchell 1967).

Despite the considerable research interest shown in age determination techniques during the last two decades (comprehensively reviewed by Taber 1969, Morris 1972, and Spinage 1973a), there is still no single completely reliable method of determining the ages of African mammals (Spinage 1973a). Further, endeavours to refine age determination techniques, which at the extreme levels of precision are of more academic than practical value (Spinage 1973a), have often been limited by procedural or statistical errors and/or omissions (Dapson 1980). Known-age animals obviate these difficulties, but are often extremely difficult, if not impossible to obtain.

A knowledge of the growth rates of individuals (which relate changes in body dimensions such as mass, height and length with age, Hanks 1972b) is of considerable value to

numerous aspects of wildlife research and management. The growth of individuals together with reproduction, forms the production of a population during the annual cycle (Sinclair 1977). In conjunction with details of age structure, growth data permit the calculations of biomass and protein production (e.g. Stewart and Zaphiro 1963; Foster and Coe 1968; Mentis 1970; von La Chevallerie 1970; Coe et al. 1975; Hirst 1974; Mentis and Duke 1976; Milligan et al. 1982) while a knowledge of the age of maximum productivity is of direct and economic relevance to the commercial exploitation of game species (Skinner and van Zyl 1970; Skinner 1973; Joubert 1974a; Smuts 1975a; Howells and Hanks 1976; Attwell 1977; Jeffery and Hanks 1981a). Growth parameters have also been extensively used in comparisons between the nutrition, condition, reproductive performance or mortality rates of populations at different times of the year (Wood et al. 1962; Mitchell et al. 1976; Mitchell et al. 1977), and in differing environments or at varying levels of management (Klein 1964, 1965, 1968, 1970; Blood and Lovaas 1966; Lowe 1971; Mitchell 1971, 1973; Hanks 1972b; Klein and Strandgaard 1972; Reimers 1972; Mitchell and Brown 1974; Roseberry and Klimstra 1975; Wegge 1975; Thorne et al. 1976; Malpas 1977; Franzmann et al. 1978; Sherry 1978; Staines 1978; Arman et al. 1978; Guinness et al. 1978a; Guinness et al. 1978b; Verme and Ozoga 1980a; Mitchell et al. 1981; Anderson 1982; Albon et al. 1983; Pemberton and Dansie 1983). Several authors have collected baseline data for comparative use within the same populations in future years (e.g. Smuts 1975a; Fairall and Braack 1976). In addition, growth data may provide estimates of the milk requirements of neonates and the energy requirements of lactating females (Robbins and Moen 1975a; Robbins et al. 1981), and assist in taxonomic studies (Howells and Hanks 1975; Attwell 1977).

Recognisable age-specific body dimensions are of considerable value in the field classification of many wildlife species (e.g. Simpson 1966; Spinage 1967, 1976a; Pienaar 1969a; Kerr and Roth 1970; Roettcher and Hofmann 1970; Croze 1972; Rowe-Rowe and Mentis 1972; Walther 1972a; Grimsdell 1973; Melton 1978a; Smuts et al. 1978;

Allen-Rowlandson 1980) and may also facilitate the correct administration of immobilizing drugs during capture operations (Attwell 1977; Jeffery and Hanks 1981a).

A second quantitative aspect of growth concerns the relationships between the dimensions (e.g. mass and height) of a single animal (Hanks 1972b), which may be used for live mass estimation (e.g. Talbot and McCulloch 1965; Krumrey and Buss 1968; Hanks 1972b; Morris 1973; Howells and Hanks 1975; Rideout and Worthen 1975; Smuts 1975a; Hanks et al. 1976; Kelsall et al. 1978; Franzmann et al. 1978; Jeffery and Hanks 1981a). In addition to estimation by linear measurements, predictive equations relating eviscerated carcass mass (or the mass of a dissected portion of the carcass) to live mass have been used in various studies (Smith and Ledger 1965; Laws et al. 1967; Attwell 1977; Albon et al. 1983).

3.1.1. Previous Studies of Age Determination and Growth in Bushbuck and Duiker

3.1.1.1 Bushbuck

Bushbuck dentition is diphyodont and similar to that of most bovids. The deciduous and permanent dental formulae have been described by Allsopp (1970) and Simpson (1973, 1974c) as follows:

$$\text{deciduous} \quad 2\left(i\frac{0}{3}, c\frac{0}{1}, pm\frac{3}{3}\right) = 20$$

$$\text{permanent} \quad 2\left(I\frac{0}{3}, C\frac{0}{1}, PM\frac{3}{3}, M\frac{3}{3}\right) = 32$$

Allsopp (1970) employed several techniques to determine the ages of bushbuck (subspecies not specified) in East Africa. Males were grouped into one of five age classes based on horn size data obtained from Hanover Zoo. Females

were classified according to tooth eruption and replacement sequences (three arbitrary classes) and by the extent of wear on permanent maxillary teeth (five classes). Tooth measurements were recorded from unspecified incisors, and included ratios of crown height to root length and the outer diameter of the incisor to the internal diameter of the pulp cavity. This latter ratio was also recorded from males. Eye lens mass was measured in both sexes, but treatment prior to weighing was not specified. Ages of males were determined from horn size up to 30 months of age, and corresponding ages were then assigned to those female classes that had comparable tooth measurement ratios and mean eye lens mass. Chronological ages, at yearly intervals, were assigned to those females in successive age classes "by extrapolation". Allsopp suggested that loss of teeth caused by root closure imposed a physiological longevity of seven years. (Spinage (1973a) however, points out that root closure may be completed relatively early in life.) Unfortunately, Allsopp's (1970) account provided little guidance in terms of procedures or recommended techniques, and contained no reference to range of values or estimates of variance for any of the techniques he employed. No distinction was made between deciduous and permanent teeth in his incisor measurements, yet according to the eruption calendar he detailed, at least one age class would have contained measurements from both types of teeth.

Simpson (1973, 1974c) provided a more refined account of tooth eruption and replacement which, based on known-age material, permitted the separation of bushbuck with deciduous dentition into one of eight distinct age classes (Table 3.1) Animals older than 30 months were assigned to one of six classes based on the amount of wear visible on specific teeth from the mandible. Ages allocated to these adult wear classes were, in the absence of known-age material, derived from the mean number of cementum annuli counted in 10 teeth (Pm4) from each representative wear class. The deposition of twin cementum annuli reflected growth during one year, and the mean age of the oldest wear class was estimated at 11,4 years (range 9-15 years).

TABLE 3.1 Tooth eruption and replacement sequence in the mandible and maxilla of the bushbuck.

Age class	Known-age (months)	Dentition			Index tooth for class	Estimated mean age (months)
		Incisiform	Premolars	Molars		
A	0-1,5	d d d d	d d d d d d	- - - - - -	Full milk dentition	1
B	4,5	d d d d	d d d d d d	E - - E - -	1st molar erupting	4,5
C	6	d d d d	d d d d d d	P - - P - -	1st molar erupted	7
D	8,5	d d d d	d d d d d d	P E - P E -	2nd molar erupting	10
E	14	d d d d	d d d d d d	P P - P P -	2nd molar erupted	14
F	19	d d d d	d d d d d d	P P - P P E	3rd molar erupting	19
G		P E d d	d d d d d d	P P E P P P	incisiforms replacing	21
H	24-26	P P P P	P E d P E d	P P P P P P	premolars replacing	26
Adult		P P P P	P P P P P P	P P P P P P	Permanent dentition	30 +

Explanation of symbols; d = deciduous tooth; E = erupting tooth; P = permanent tooth. (After Simpson 1973)

For analyses of eye lens mass and horn growth data, Simpson combined several of the subadult eruption and replacement classes and altered the mean ages of these accordingly. Due to considerable overlap between the majority of subadult and adult classes, fresh eye lens mass was found to be of limited use as an age determination technique. Horn size and shape proved to be a useful

criterion for assessing the ages of subadult and young adult males in the field. However, Simpson (1972,1973) found considerable variation due both to individual growth and to differential wear and recommended the use of additional (unspecified) criteria in classifying mature animals. Having compared the ages of individuals estimated from cementum annuli and from horn growth checks, Simpson (1972) concluded that the latter method provided an accurate means of age determination for bushbuck (T.s.ornatus).

Morris (1973) studied the same subspecies and noted considerable differences between his adult wear criteria and those of Simpson (1973). Attempts to section teeth for cementum annuli counts met with limited success and Morris subsequently rejected his own wear criteria and made extensive use of those detailed by Simpson (1973). Mean eye lens mass differences between males and females were significant in several of the age classes examined, and Morris concluded that individual variation limited the value of eye lens mass for age determination purposes. Horn growth checks were personally identified by Simpson, but Morris considered these to be inaccurate, since ages were overestimated by this method when compared to ages of the same individuals estimated by tooth wear.

Aspects of growth in the bushbuck have been examined by both Simpson (1973, 1974c) and Morris (1973). Simpson found that the relative size and proportion of the body provided a means of separating juveniles, subadults and adult females in the field, but concluded that such evaluations were qualitative and could only be used reliably with experience. Assessment of ages of males in the field could also be achieved to some extent by horn shape and size criteria.

Simpson (1973, 1974c) and Morris (1973) found that males were significantly larger than females in all of the parameters they examined. Simpson ignored these differences in the production of growth curves for shoulder height, hindfoot length and ear length, and omitted details of the processes used to derive these curves. Morris (1973) using

the Von Bertalanffy growth equation, treated male and female data separately and provided asymptotic values for six of the seven parameters examined. Growth equations were not detailed however, and the ages at which asymptotic values were attained were not given. With the exception of body mass, growth parameters recorded from both studies were in close agreement. Individuals from the population studied by Morris were considerably heavier however, and in contrast to Simpson's results, where males attained asymptotic mass at approximately 60 months of age, continued to gain weight throughout life. Morris (1973) also examined the relationship between body mass and girth measurement but concluded that such a relationship was imprecise for mass estimation purposes.

3.1.1.2 Duiker

The dental formulae for duiker have been detailed by Riney and Child (1960) and are identical to those for bushbuck. These authors developed nine broad age classes, six of which were based on tooth eruption and three concerned with the extent of tooth wear. Chronological ages were assigned only to those classes with erupting dentition. Riney and Child (1964) later examined horn length as a technique for age determination, but concluded that due to rapid initial growth and individual variation, the method was of limited value in the field even for classifying six month old animals.

Simpson (1971) investigated the presence of horn growth checks as a potential means of age determination for duiker. Distinct checks were found in 78% of the mature animals he examined, but were indistinct in many subadult horns. Causal factors were not examined however, and no attempts were made to relate these checks to age.

The most comprehensive account of age determination in this species has been provided by Wilson et al. (1984). Age determination was investigated by analysis of tooth eruption

and replacement sequence, tooth wear and cementum annuli in a unique collection of 48 known-age skulls and also by examination of post-natal body growth in individuals of known age. Twelve tooth eruption and replacement classes were identified from the mandible (Table 3.2) and ten from the maxilla (Table 3.3). These authors found little variation in the age of eruption and replacement of all of the molariform teeth, which were fully erupted and in wear by 26 months of age. Eruption times of the incisiforms were extremely variable however, and this variability, together with the difficulties experienced in distinguishing between deciduous

TABLE 3.2 Tooth eruption and replacement sequence in the mandible of the common duiker.

Age class	Known-age (months)	Dentition										Recommended allocation of chronological age (months)
		Incisors			Canine	Premolars			Molars			
		1	2	3	1	2	3	4	1	2	3	
1	0	d	d	d	d	e	e	e				0
2	1-3	d	d	d	d	d	d	d	e			1,5
3	2,5-3	d	d	d	d	d	d	d	E			3,0
4	4,5	d	d	d	d	d	d	d	P			4,5
5	7	d	d	d	d	d	d	d	P	e		7,0
6	8,5-10,5	d	d	d	d	d	d	d	P	E		9,0
7	9-10	d	d	d	d	d	d	d	P	P		10,0
8	15-20	d	d	d	d	d	d	d	P	P	e	17,5
9	17-23	d	d	d	d	d	d	d	P	P	E	20,0
10	22-25	d	d	d	d	d/e	d/e	d/e	P	P	P	24,0
11	26-48	d	d	d	d	P	P	P	P	P	P	30,0
12	34-37	d/P	d/P	d/P	d	P	P	P	P	P	P	35,0
13	60-older	P	P	P	P	P	P	P	P	P	P	60,0+

Explanation of symbols; d = deciduous tooth; d/e = deciduous tooth still present, with permanent tooth erupting below; d/P = erupting incisor, I1 to I3 may be at any stage from d/e to just P; e = permanent tooth just erupting, only cusps or tips visible above bone; E = erupting permanent tooth, all four cusps well above bone but not fully erupted; P = fully erupted permanent tooth. (After Wilson et al. 1984).

TABLE 3.3 Tooth eruption and replacement in the maxilla of the common duiker.

Age class	Known-age (months)	Dentition						Recommended allocation of chronological age (months)
		Premolars			Molars			
		2	3	4	1	2	3	
1	0	e	e	e				0
2	1-2,5	d	d	d	e			2,0
3	3-4,5	d	d	d	E			4,0
4	4,5-7	d	d	d	P			6,0
5	9	d	d	d	P	e		8,5
6	8,5-10,5	d	d	d	P	E		10,0
7	10-18	d	d	d	P	P		15,0
8	18-23	d	d	d	P	P	e	21,0
9	22,5-25	d/e	d/e	d/e	P	P	E	24,0
10	26-older	P	P	P	P	P	P	26,0+

Symbols as in Table 3.2. (After Wilson et al. 1984)

and permanent incisiforms, imposed severe limitations on the reliability of this technique for age determination in older animals (Classes 11 to 13, Table 3.2).

In their study of tooth wear, which involved all three molars from 14 known-age duiker, Wilson et al. (1984) found a negative correlation between crown height and age. These authors concluded however, that such a linear relationship should be regarded as provisional since only four animals

were four years of age or older. Further, the authors warned against the direct extrapolation of their wear data to populations elsewhere, where phenotypic and/or genotypic differences in tooth wear might exist.

Although cementum annuli were detected by these authors, these lines were very indistinct and demonstrated a considerable degree of splitting and merging to the extent that quantification was impossible in every tooth examined.

In their study of body growth, which involved use of the Von Bertalanffy growth equation, Wilson et al. (1984) found that there was little difference between the sexes in the ages at which asymptotes were reached for ear length, hindfoot length, hoof length, tail length and total body length. Although body mass and shoulder height growth was prolonged in both sexes, asymptotes for these parameters were attained at a later age in males. Further, these were the only parameters where males were not significantly smaller than females. Because the asymptotes of growth were reached at such an early age, and as a result of the considerable variation between individuals, these authors concluded that body and horn growth were of limited value as methods of age determination in the duiker.

3.1.2 Methods currently employed in the determination of age and growth

Age determination methods can be divided into two categories. The first of these concerns the separation of individuals into relative age groups, while the second involves methods of allocating chronological ages to these classes (Spinage 1973a). This latter aspect is commonly achieved by reference to known-age material, but where absent, Spinage (1973a) suggests the use of as many complementary methods as possible.

The most common method of determining the ages of young individuals involves the use of tooth eruption and

replacement schedules. These have been documented for a wide variety of mammals (e.g. Fuller 1959; Bergerud 1970; Goddard 1970a; Roettcher and Hofmann 1970; Robinette and Archer 1971; Joubert 1972; Grimsdell 1973; Miller 1974a; Hitchins 1978; Smuts et al. 1978; Ludbrook and Ludbrook 1981), with or without reference to known-age material. Although eruption and replacement times may be influenced by environmental or genetic factors, variations between individuals from different populations are usually insignificant (Miller 1972; Spinage 1973a). Since the eruption and replacement sequences for bushbuck and duiker, described respectively by Simpson (1973) and Wilson et al. (1984), were both based on known-age animals, these were considered to be the most accurate means of subadult age determination for this study. Attrition of the permanent teeth provides the most convenient means of age determination in adult animals (Spinage 1973a). The extent of wear may be assessed visually and then compared to wear patterns from known-age animals or to a series of classes each with easily separable characteristics (e.g. Simpson 1966, 1973; Mitchell and Youngson 1968; Roettcher and Hofmann 1970; Lombaard 1971; Attwell and Jeffery 1981).

Alternatively, wear may be evaluated quantitatively by measurements of specific teeth (e.g. Spinage 1972a, 1973a, 1976a, 1979; Lowe 1967; Hall-Martin 1976; Attwell 1980; Jeffery and Hanks 1981b; Wilson et al. 1984). Although the use of measurements may remove observer bias, it cannot correct for varying rates of wear and this remains a pseudo-objective method (Spinage 1973a). Since highly variable rates of wear were noted during initial dental inspections of both bushbuck and duiker, attrition measurements were not considered in this study. Teeth exhibiting the most variable rates of wear in these two species corresponded to those found in several other ungulate age determination studies, namely the incisors (Mitchell and Youngson 1969; Spinage 1973a) and teeth from the middle of the molariform tooth row (Attwell 1980; Attwell and Jeffery 1981).

The detection of incremental growth rings in dental

tissues (usually the dental cementum) has become a popular method of adult age determination in recent years (e.g. Mitchell 1963, 1967; Spinage 1967, 1976b; Robinette and Archer 1971; Simpson 1973; Miller 1974a, 1974b; White 1974; Turner 1977; Gasaway et al. 1978). Provided that deposition rates are known, the method provides a reliable means of absolute age assignment (Attwell 1980) and numerous studies have shown the technique to be more accurate than other methods of age estimation (Keiss 1969; Erickson et al. 1970; Gilbert and Stolt 1970; Kerwin and Mitchell 1971; Thomas and Bandy 1975; Thomas 1977; Hitchins 1978; Jeffery and Hanks 1981b). However, while the deposition of cementum annuli has often been related to environmentally stressful periods (Mitchell 1963, 1967; Reimers and Nordby 1968; Grimsdell 1973; Miller 1974b; Spinage 1976b; Turner 1977), it is still uncertain which factors are primarily responsible for causing the incidence of periodic growth in the cementum (Grimsdell 1973; Spinage 1976b). Even in known-age animals close agreement between cementum annuli counts and age is not always achieved (Ransom 1966; Goddard 1970a) and the difficulties in interpreting cementum annuli (Lowe 1967; Miller 1974b; Smuts et al. 1978; Leader-Williams 1979) together with other sources of error (Gasaway et al. 1978) have demonstrated that this should not be regarded as a definitive technique. Nevertheless, in the absence of known-age material, the method was investigated during this study.

The rates at which cementum annuli are deposited have been studied by labelling teeth with tetracyclines, which chelate with calcium ions wherever active calcification is taking place (Spinage 1973a). Although the technique was considered by Spinage (1967, 1973a) to have high potential, Smuts et al. (1978) obtained unsatisfactory results in their study and abandoned the method. Since, at the start of field work, there was no guarantee that individuals could be recovered at a later date, vital staining was not considered suitable for this study. Tooth impressions, which permit the accurate assessment of tooth wear rates over known intervals of time (Flyger 1958; Barnes and Longhurst 1960; Spinage

1967, 1973a; Melton 1978a; Eltringham 1979) were similarly dismissed for the same practical reason.

Other established methods of age determination that do not involve the use of teeth include eye lens mass, ossification of epiphyseal cartilage, horn annuli and rates of body growth. The eye lens is an ectodermal structure and grows continuously throughout life. Since the lens is not subjected to any form of wear, its mass will therefore increase with time. Several studies have shown that age determination by eye lens mass is most accurate for small mammals, (Friend 1968; Morris 1972; Dubock 1979; Perrin 1979) but may also provide a reliable estimation of age in deer (Longhurst 1964). This method was therefore considered worthy of investigation during the course of this study. Because of the biochemical techniques involved, accumulation rates of insoluble eye lens proteins as a means of age determination (Otero and Dapson 1972; Ludwig and Dapson 1977) were considered to be beyond the scope of this study.

The cessation of growth in the long bones and vertebrae, as indicated by the state of ossification of the epiphyseal cartilage, has been used as an age determination criterion in several wildlife studies (Lombaard 1971; Morris 1972; Dubock 1979). The method is limited however, since it only permits separation of juveniles from adults (Attwell 1977). Since such distinction can more readily be achieved by reference to tooth eruption and replacement, the technique was not considered in this study.

Horn growth checks have been used to estimate the ages of a number of American bovid species (e.g. Geist 1966a; Taber 1969; Gonzales 1976). Simpson (1971) found similar growth checks in a number of African antelope (including duiker), and established that in bushbuck, and in four other Tragelaphines, such checks were formed seasonally and were sufficiently pronounced to permit evaluation. Although personal unpublished results from previous studies of the greater kudu differed from Simpson's (1972) findings, this method of age determination was included in the present

study.

Where growth studies are concerned with changes in mass, height, or length with age, these changes are usually represented as growth curves. Difficulties may be experienced in the plotting of such curves when data are non-linear, and although these may be fitted by eye (e.g. Pienaar 1969a; Kerr and Roth 1970; Lowe 1971; Franzmann et al. 1978), a more objective means of fitting curves to growth data is offered by the Von Bertalanffy growth equation (Hanks 1972b; Smuts 1975a; Attwell 1977; Grobler 1978; Anderson 1978). Such an approach was adopted in this study. Broad growth parameters such as body and horn dimensions, together with changes in pelage, etc., were also used to classify ages in the field.

3.2 METHODS

3.2.1 Source of Material

The majority of the material used for age determination and growth purposes came from 132 bushbuck (68 males and 64 females) and 118 duiker (61 males and 57 females) all of which were randomly shot within the extensive study area. A further 36 bushbuck (19 males and 17 females) and 12 duiker (8 males and 4 females) that had recently died from other causes (e.g. road kills, during capture operations, natural mortalities, etc.) within Weza State Forest, were added to this sample.

3.2.2 Tooth Eruption and Replacement Sequence

In the absence of known-age material, reference was made to the eruption and replacement sequences detailed by Simpson (1973) and Wilson et al. (1984) for bushbuck and duiker respectively. All bushbuck skulls that did not have fully erupted permanent dentition were assigned to one of Simpson's (1973) eight eruption classes as shown in Table 3.1.

Difficulties experienced in distinguishing between deciduous and permanent incisors necessitated slight changes in the classification recommended by Wilson et al. (1984) for duiker, and their age classes of 10, 11 and 12 (Table 3.2) were combined, with a mean estimated age of 27,0 months. Only mandibles with clearly erupting premolars or with obviously worn incisiforms were placed within this class, which for continuity was designated class 10-12. The criteria of Wilson et al. (1984) for tooth eruption and replacement in the maxilla (Table 3.3) were not modified for this study, and were consulted when tooth eruption patterns in the mandible were intermediate.

3.2.3 Tooth Attrition

Initially, attempts were made to place each of 134 bushbuck mandibles, all with fully erupted permanent dentition, into one of Simpson's (1973) six tooth wear classes. This classification was found to be inadequate however, since many of the mandibles from the Weza population exhibited a combination of features that Simpson (1973) had isolated as diagnostic characteristics for each of his age classes. Consequently, Simpson's (1973) classification was rejected, and new criteria, based on the degree of wear and progressive disappearance of the infundibula on specific molariform teeth, were devised.

The broad age classes adopted by Riney and Child (1960) for duiker were also regarded as inadequate for this study and a more detailed classification, involving similar (but not identical) criteria to those used for bushbuck, was established. Sixty-five duiker mandibles, all with permanent dentition, were subsequently placed into one of six tooth attrition classes.

3.2.4 Cementum annuli

Heavily worn first and third molars were extracted from

the mandible of a relatively old female bushbuck. Approximately 2 mm sections were then cut through each tooth using a water-cooled circular saw with a diamond blade. These sections, which were taken sagittally in the first molar and along the transverse axis of the third molar, were polished on an electric grinding wheel, using successively lighter grades of carborundum. To prevent mechanical damage as the section became thinner, one side of the section was polished first and then adhered to a microscope slide with epoxy resin before commencing on the other surface. The completed slides were then moistened and examined for cementum lines using a binocular microscope under both reflected and polarised light.

All three worn molars were also extracted from the left half of a duiker mandible, fixed in 10% buffered neutral formalin and decalcified in 5% nitric acid plus 5% (by volume) citric acid. These teeth were dehydrated, embedded in paraffin wax, sectioned at 7-15μm and stained with Haris's haematoxylin and eosin. The stained sections were examined microscopically with transmitted light for the presence of cementum annuli.

3.2.5 Eye Lens Mass

Unless obviously damaged, lenses from both eyes were removed shortly after death, once each eye had been dissected out of the skull, and immediately fixed in 10% formalin. After variable periods of storage, lenses were freed of any ciliary or suspensory tissue and dried in a ventilated oven kept at 100°C for one month. Damaged, discoloured or distorted lenses, or those with obvious cataracts, were discarded prior to weighing, which was done once several lenses had been cooled in a dessicator over silica-gel. Individual lenses were weighed to 0,0001g on an electric balance and replaced in the oven. Weighing was discontinued once each lens had reached a constant mass, which was invariably achieved within six weeks.

3.2.6 Growth

Morphometric data were obtained from 256 randomly culled animals (138 bushbuck and 118 duiker) immediately after death. In order to prevent or reduce damage to the head or carcass, animals were shot through the neck with a high velocity (0,270 calibre) sporting rifle. Apart from the neck, measurements were not recorded from those parts of the body where tissue damage (caused by bullet expansion) was severe, or where the penetration of a bullet fired from an oblique angle resulted in damage to any limb or girdle. Such damage was more frequently caused to young animals, and to a lesser extent to adult duiker and female bushbuck.

Measurements, using a flexible tape, were recorded to the nearest 1mm for ear length, tail length, hindfoot length (cum ungue), girth, shoulder height and total body length, following the procedures described by Ansell (1965). Shoulder height and total body length were recorded "over the curves" as suggested by Smuts (1975a). Horn lengths of both bushbuck and duiker males were recorded using the Rowland Ward system of trophy measurement (Bryant 1984), once the skulls had been thoroughly cleaned. At the same time, horns were also examined for the presence of growth checks as described by Simpson (1971, 1972). Carcasses were taken to the field laboratory once culling operations were completed (sometimes up to several hours after death) and then weighed to the nearest 0,25 kg on a 100 kg spring balance. The "larder" or "carcass" mass (Mitchell et al. 1977; Mitchell and Crisp 1981; Mitchell et al. 1981; Clutton-Brock et al. 1982a; Albon et al. 1983) was recorded from several bushbuck and duiker that were reweighed less blood and alimentary tract. During routine post mortem analysis, the embryo or foetus of any pregnant female was weighed to the nearest 0,01g on a triple beam balance for age determination purposes (as detailed in Chapter Five).

Mass and length data were analysed by computer (University of Natal IBM 1130) using the program developed by Hanks (1972b) for the Von Bertalanffy (1938) growth equation.

Growth in mass with age in the Von Bertalanffy equation takes the cubic form:

$$mt = M\infty(1-e^{-k[t-to]})^3$$

where:

mt = mass at age t

$M\infty$ = asymptotic mass; the maximum mass that an animal can attain under given conditions

k = coefficient of catabolism, a constant representing the catabolism of body materials

t = age of animal

to = theoretical age at which the animal would have zero mass with the same growth pattern as that observed in later life.

Growth in length of any specific body measurement takes the non-cubic form:

$$lt = L\infty\,(1-e^{-k[t-to]})$$

(Howells and Hanks 1975).

The program of Hanks (1972b) computed the three coefficients $M\infty$ (and $L\infty$), k and to and from observed data, and for each age class, provided a fitted value of the growth parameters under consideration. These fitted values were then used to draw growth curves.

3.3 RESULTS

3.3.1 Tooth Attrition

3.3.1.1 Bushbuck

With the exception of the oldest age class, tooth attrition patterns were similar for both males and females, and the mandibles of both sexes were combined in devising the tooth attrition classes. Using the diagnostic features describing each class given below, an independent observer

was able to place over 95% of the 134 mandibles into the same age classes as the author. Where disagreement occurred, this involved mandibles from the younger classes and was invariably associated with the premolars (particularly Pm4) which showed considerable variation in morphology and hence wear.

Five classes were defined, in ascending order of tooth attrition, as follows:

Class 1

The hypoconids and protoconids of the molars show very slight wear and the posterior infundibulum of M3 may have disappeared. Slight wear may occur on the metaconids and paraconids of Pm3 and Pm4, while the hypoconids and adjacent lophs are intact (Fig. 3.1).

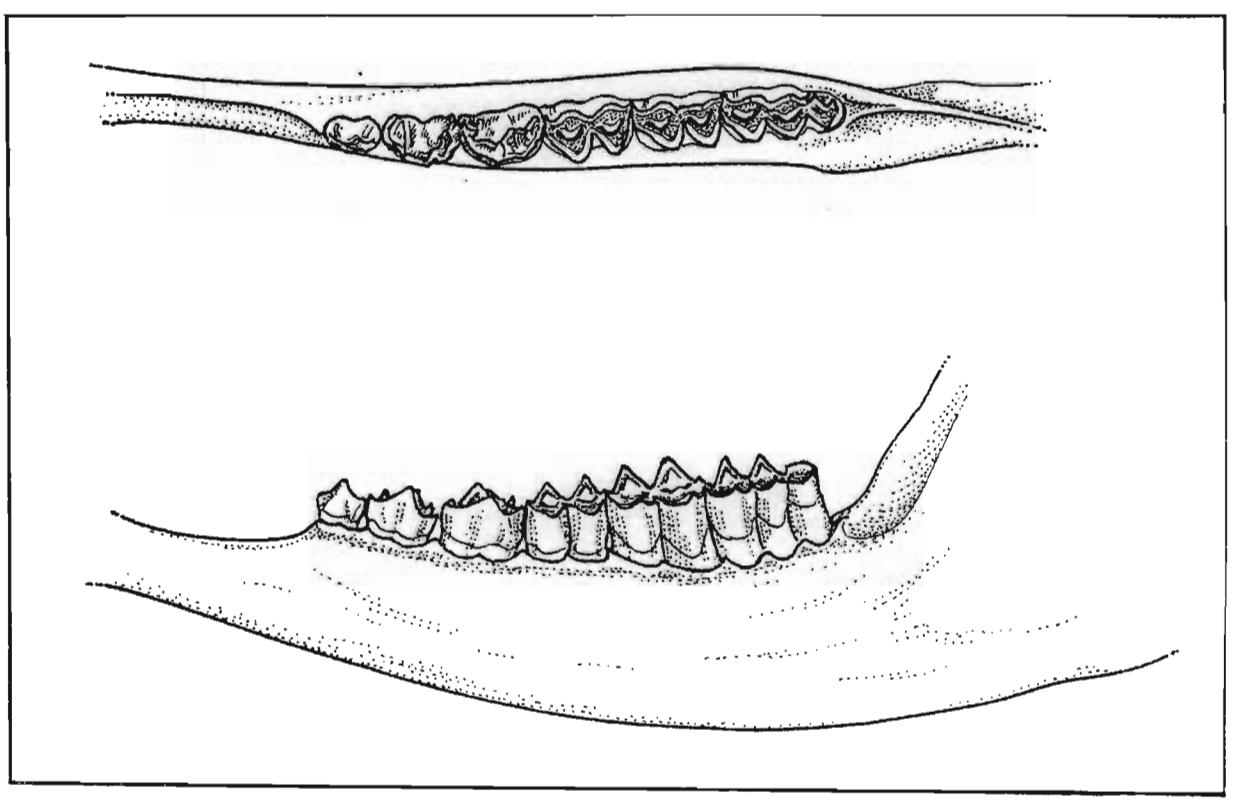


FIGURE 3.1 Bushbuck Age Class 1: occlusal and lateral view of left mandible (x1).

Class 2

Wear has reduced the height of the hypoconid and protoconid of M1, but both infundibula remain in this tooth. The lingual cusps of M2 and M3 are still sharp and show little wear. Uneven wear has occurred on Pm3 and Pm4, particularly on the metaconids and paraconids, with the infundibula often separated from the margin of the tooth (Fig. 3.2).

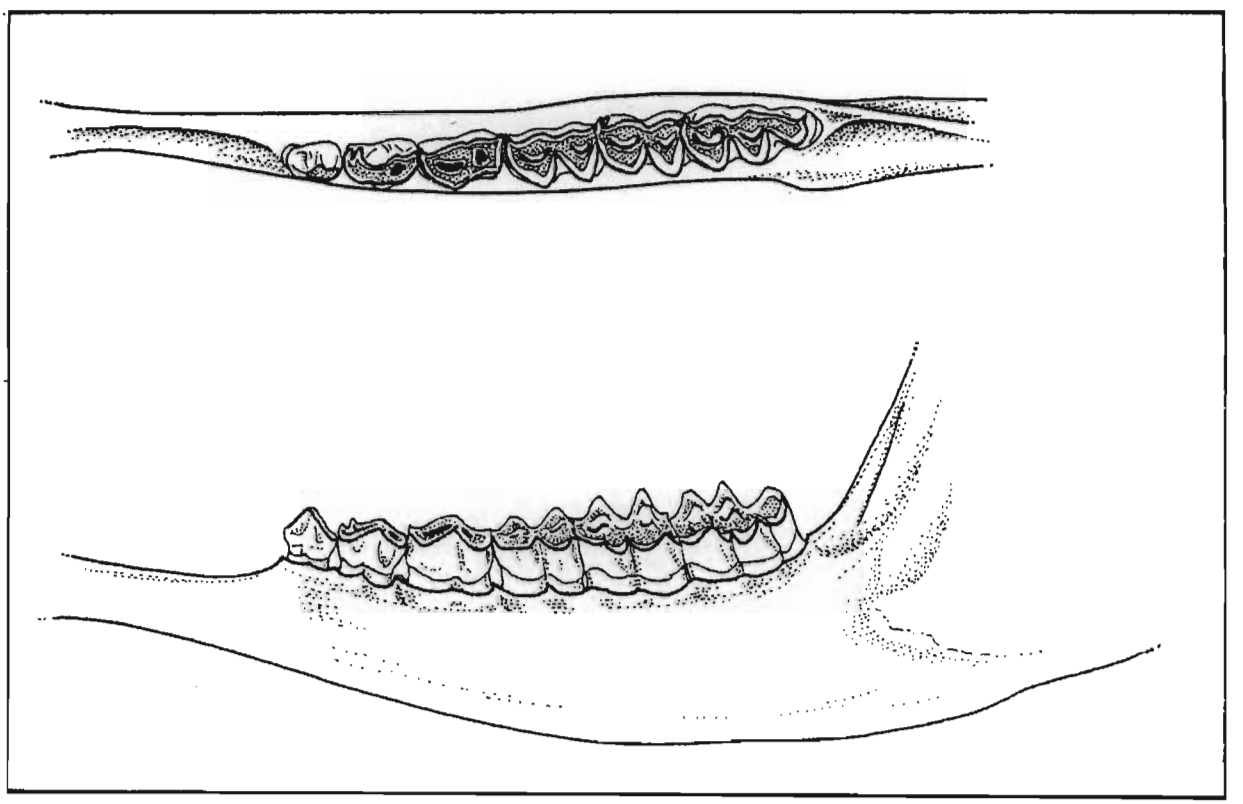


FIGURE 3.2 Bushbuck Age Class 2: occlusal and lateral view of left mandible (x1).

Class 3

The anterior infundibulum on M1 has disappeared (or only faint traces remain) but the posterior infundibulum of M1 is still clearly visible on both halves of the mandible. Variable wear has occurred on all of the cusps and lophs of the premolars forming angular facets or a flattened occlusal surface (Fig. 3.3).

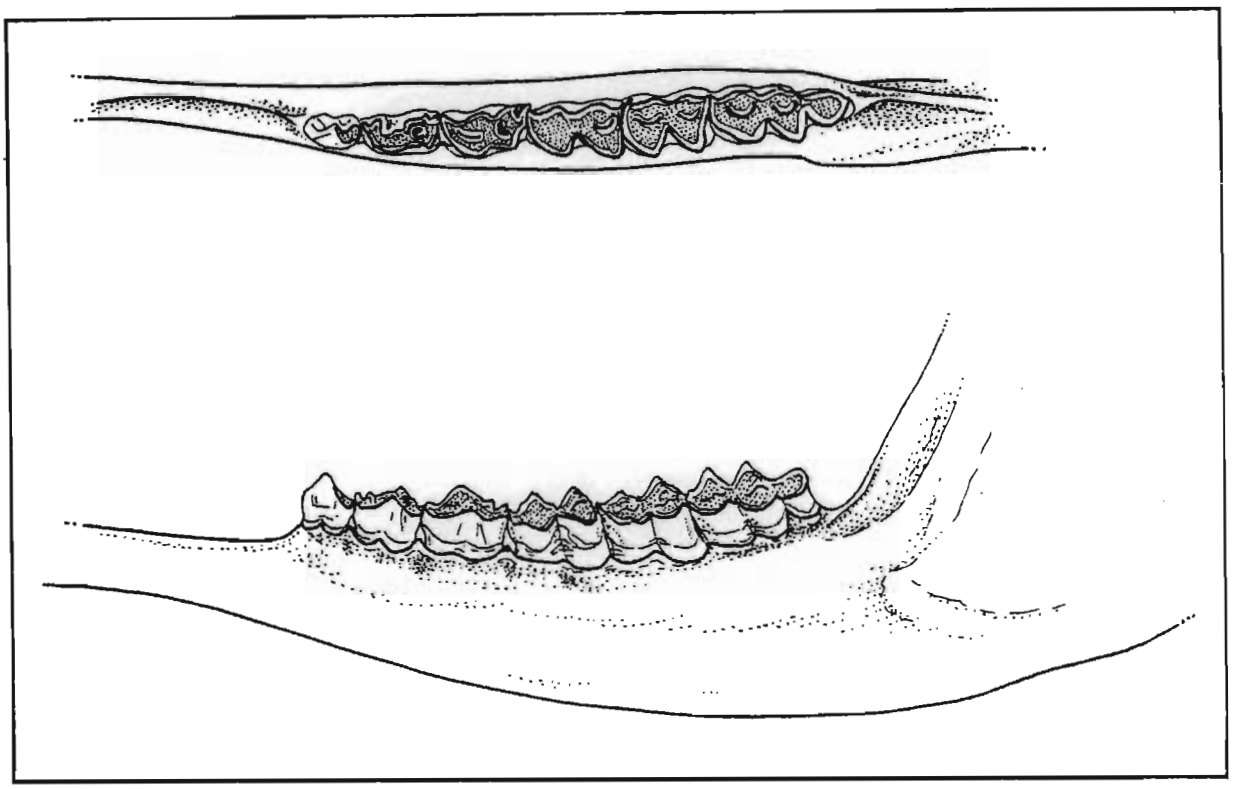


FIGURE 3.3 Bushbuck Age Class 3: occlusal and lateral view of left mandible (x1).

Class 4

Dentine is exposed throughout the length of M1 due to the disappearance of the posterior infundibulum. The anterior infundibulum of M2 is reduced in size (Fig. 3.4).

Class 5

i) Females

Infundibula are absent from all of the molar teeth and are greatly reduced in size on all the premolars. A sharp crest remains at the posterior of M3 due to the scalloped effect of wear between this tooth and its maxillary counterpart (Fig. 3.5).

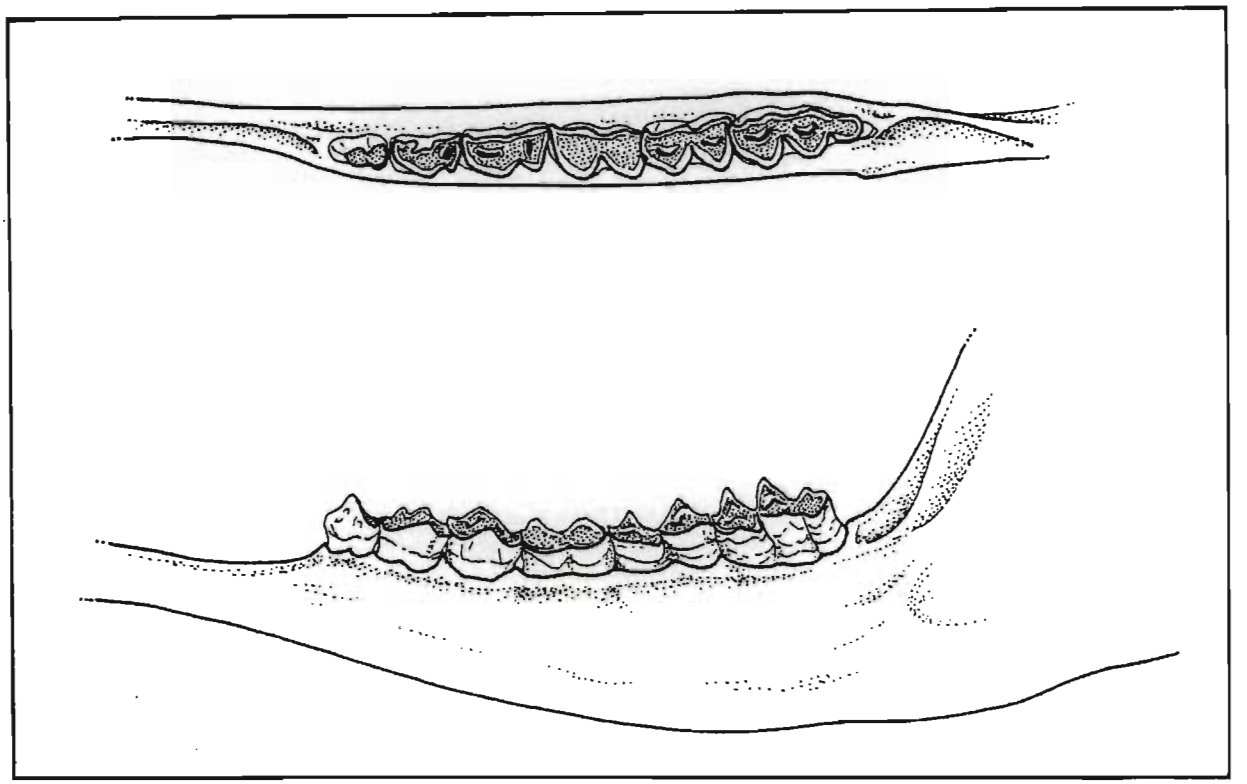


FIGURE 3.4 Bushbuck Age Class 4: occlusal and lateral view of left mandible (x1).

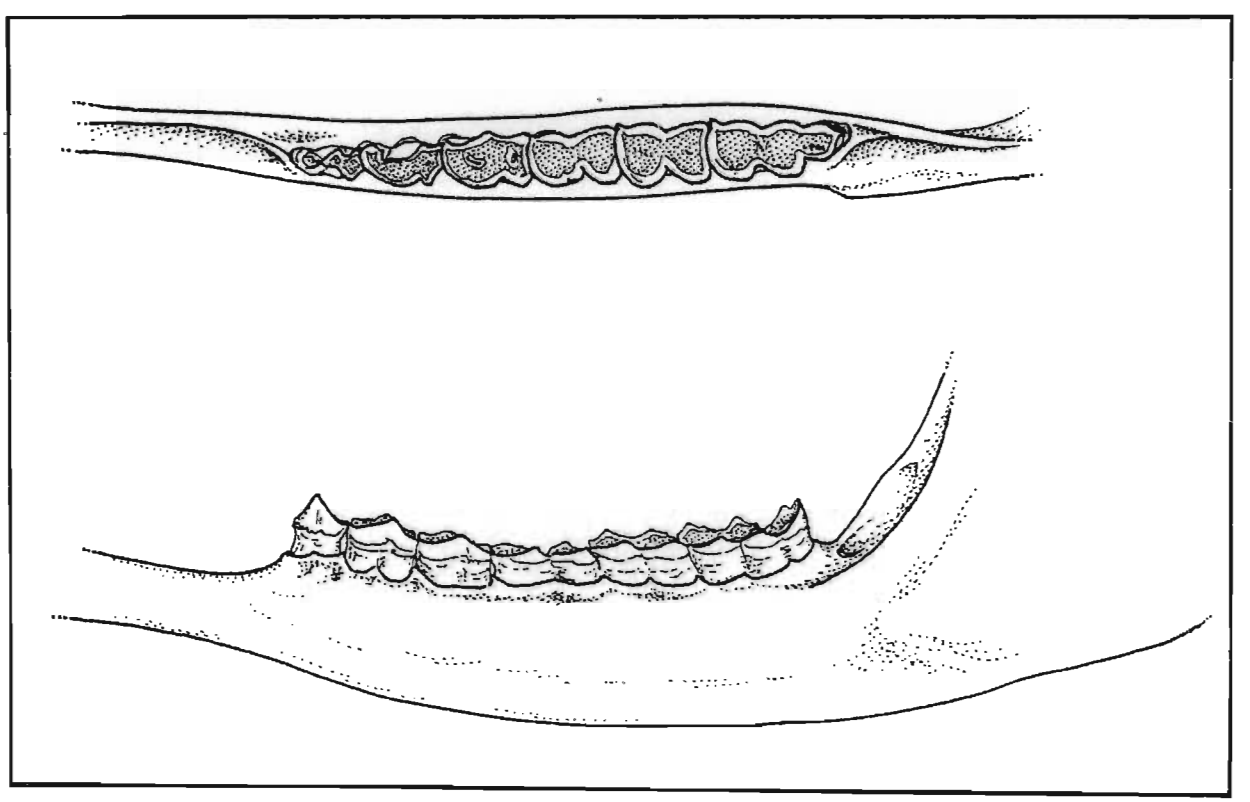


FIGURE 3.5 Bushbuck Age Class 5 (females): occlusal and lateral view of left mandible (x1).

ii) Males

As for females, or more commonly, uneven and excessive wear in the central portion of the molariform tooth row, resulting in the breakdown of the teeth, particularly M1, and the exposure of the molar roots (Fig. 3.6).

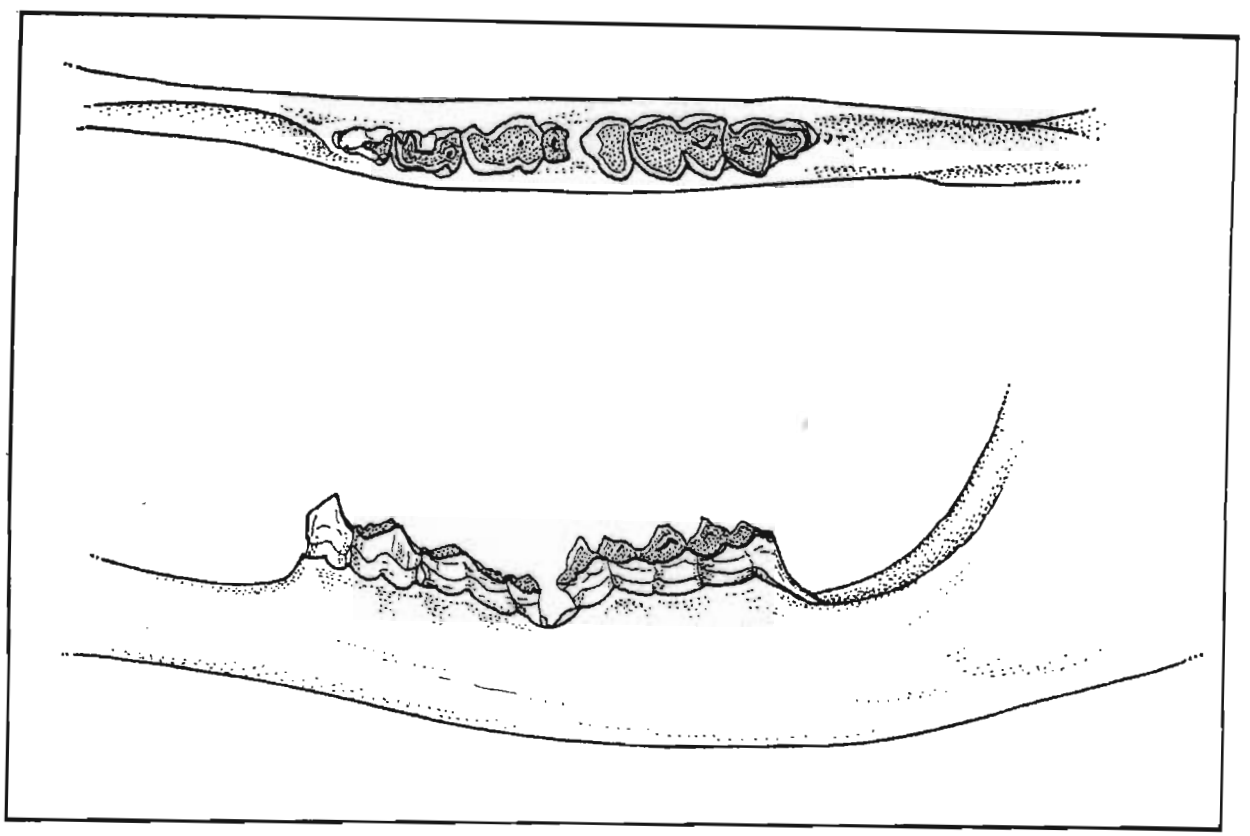


FIGURE 3.6 Bushbuck Age Class 5 (males): occlusal and lateral view of left mandible (x1).

3.3.1.2 Duiker

Tooth attrition patterns were similar for both male and female duiker, and the procedures described for bushbuck were also applied to this species. Six tooth wear categories were defined using the following criteria:

in the latter, attrition of the hypoconid and the metaconid tends to narrow the occlusal width in the central to posterior portion of the tooth (Fig. 3.9).

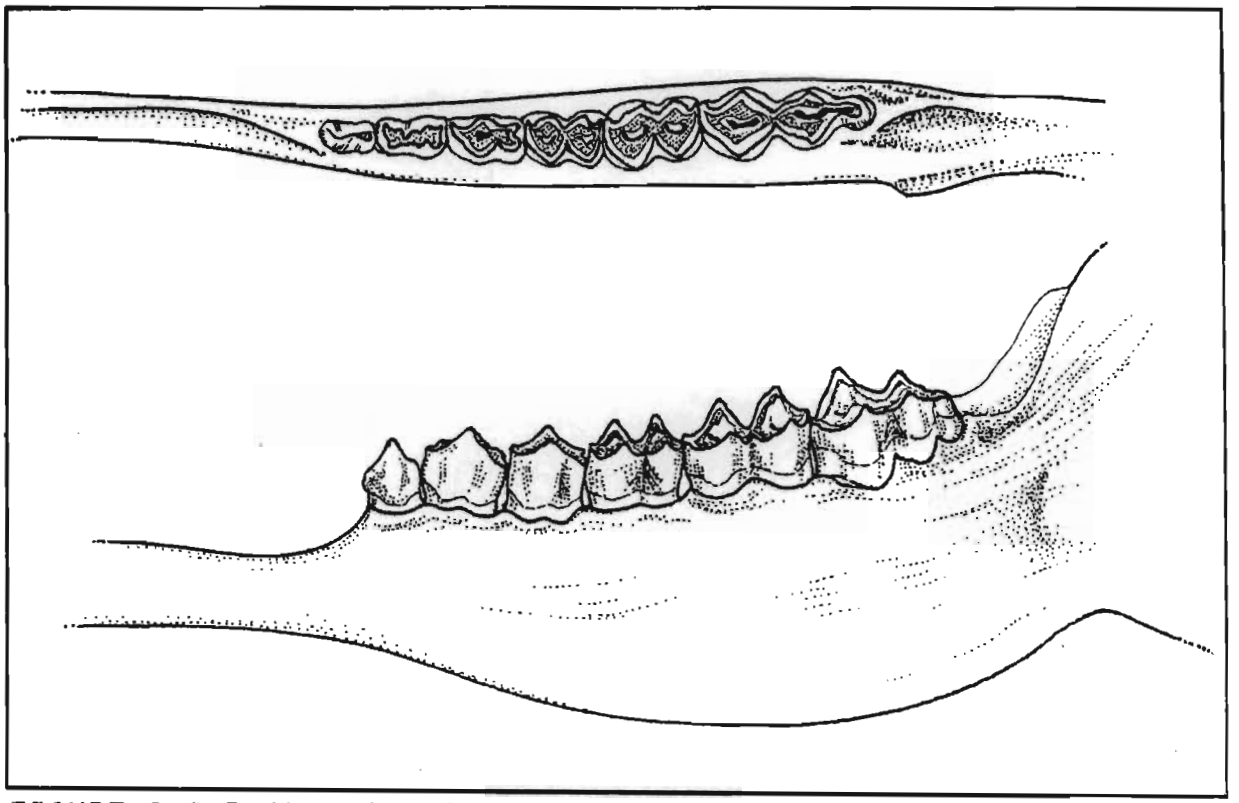


FIGURE 3.8 Duiker Age Class 14: occlusal and lateral view of left mandible (x1,5).

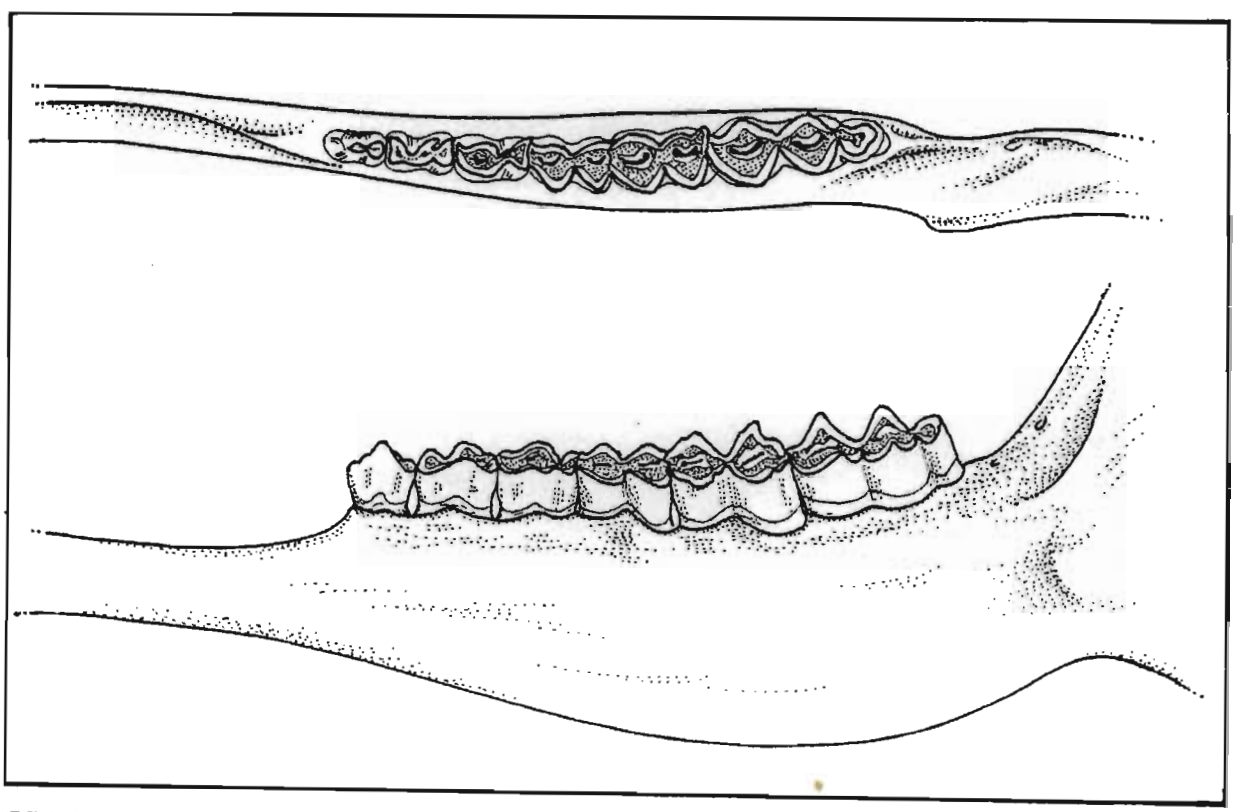


FIGURE 3.9 Duiker Age Class 15: occlusal and lateral view of left mandible (x1,5).

Class 16

Additional wear has decreased the heights of the lingual cusps of all the molars. Both anterior and posterior infundibula of M1 are reduced in size but remain clearly visible. Distinct wear is evident along the entire occlusal surface of Pm3 (Fig. 3.10).

Class 17

The anterior infundibulum of M1 is absent while faint traces of the posterior infundibulum may or may not still remain. Infundibula are intact on all the other molars and on Pm4 (Fig. 3.11).

Class 18

Considerable wear is evident throughout the entire tooth row, forming a more or less continuous line of dentine. Infundibula from all of the molariform teeth are either greatly reduced in size of absent (Fig. 3.12).

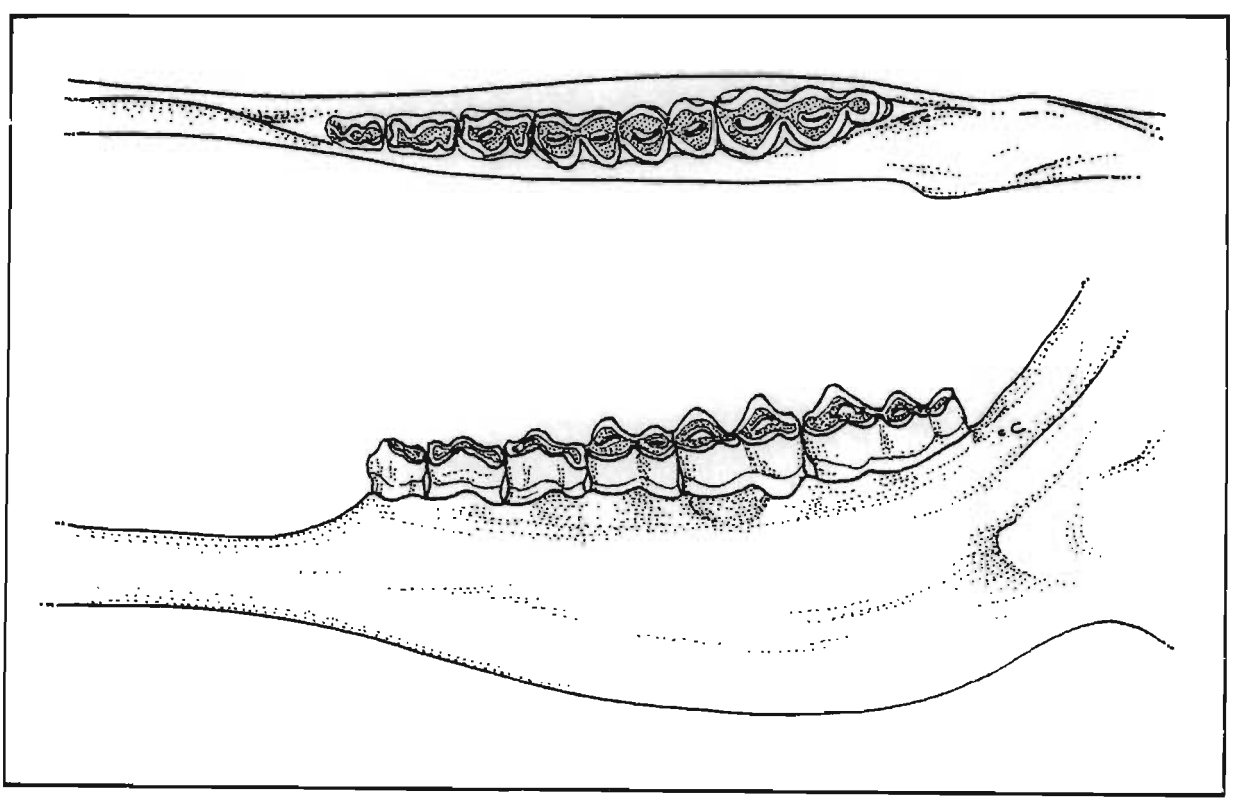


FIGURE 3.10 Duiker Age Class 16: occlusal and lateral view of left mandible (x1,5).

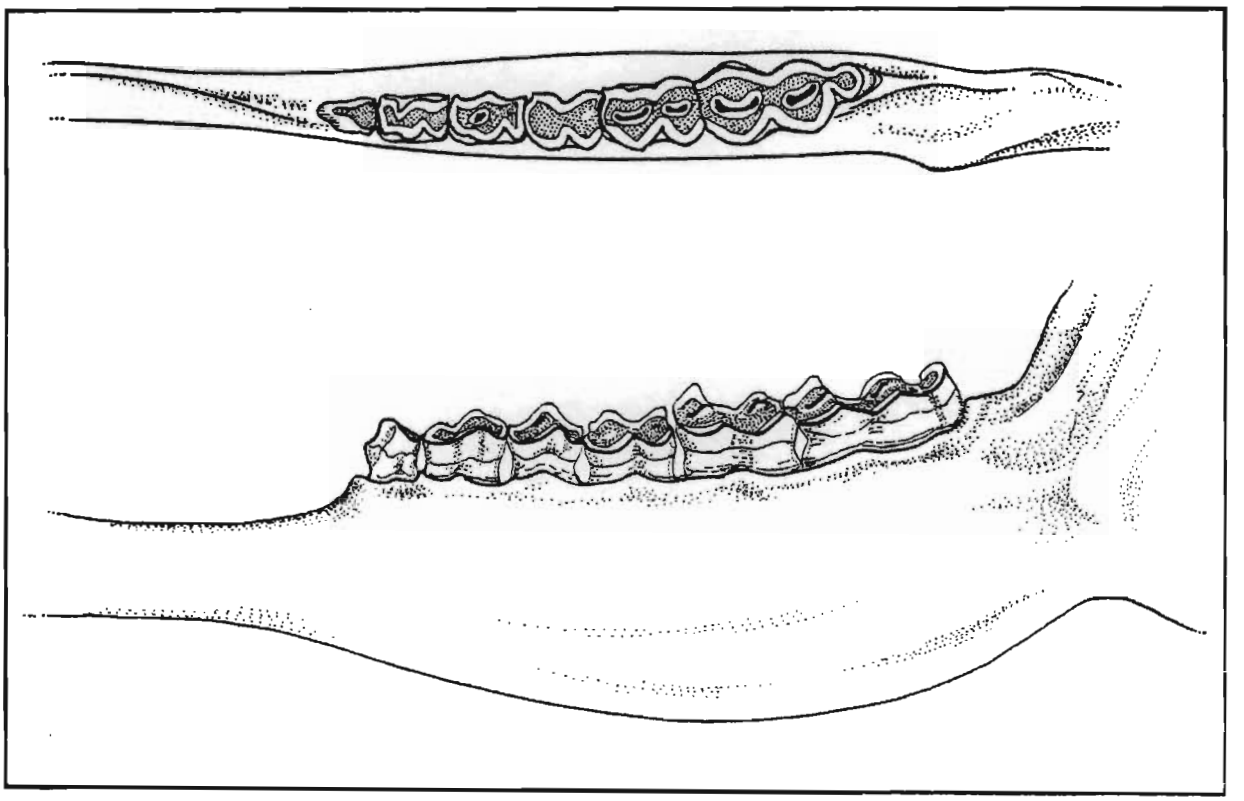


FIGURE 3.11 Duiker Age Class 17: occlusal and lateral view of left mandible (x1,5).

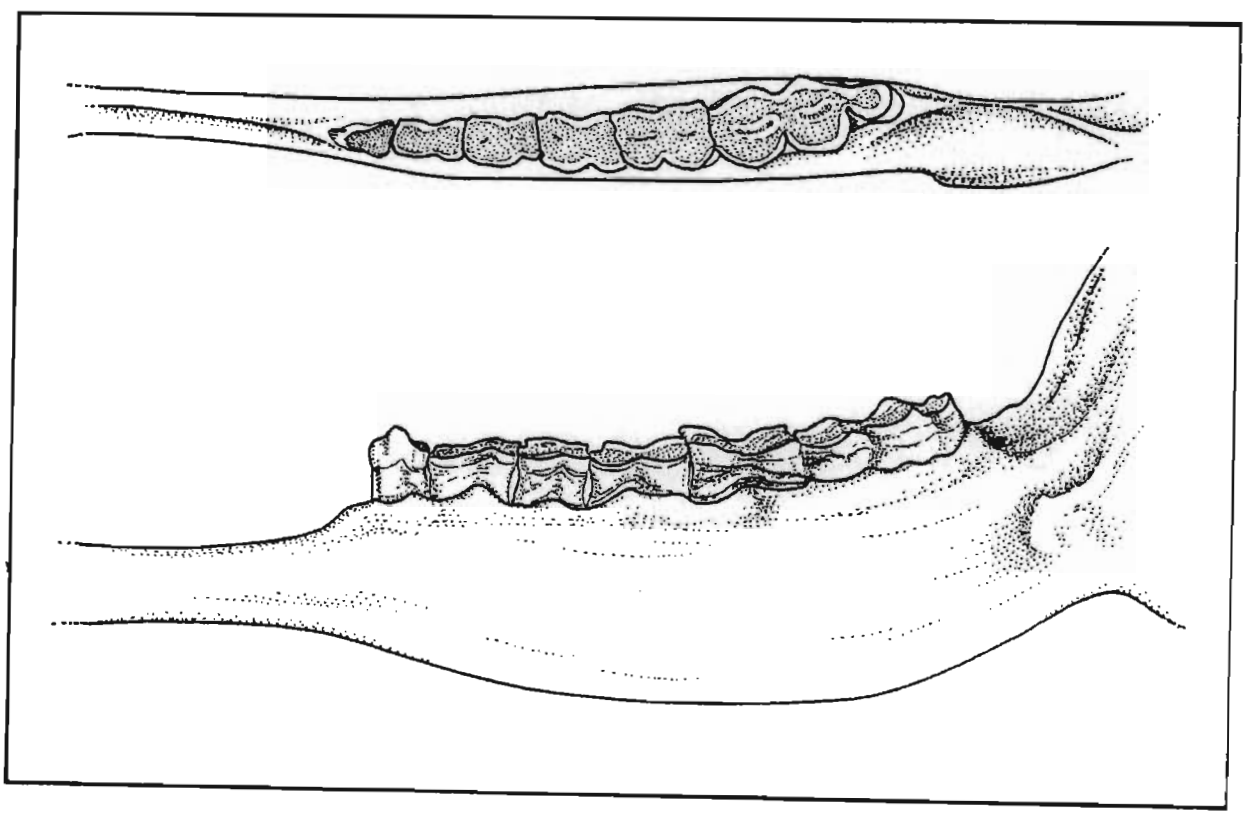


FIGURE 3.12 Duiker Age Class 18: occlusal and lateral view of left mandible (x1,5).

3.3.2 Cementum Annuli

Although the polished undecalcified sections were prepared from heavily worn teeth, few lines were visible in either of the bushbuck molars examined under reflected or polarised light. Where lines were visible, these were confined to relatively small areas of the root or cementum pad, and interpretation of their origin or actual number was, at best, extremely subjective.

Cementum lines were also detected in the decalcified sections of molars from duiker, but these too were indistinct and exhibited a considerable amount of merging and splitting. None of the three observers who examined this material were able to interpret the cementum lines quantitatively. Cementum annuli were therefore considered to be totally unsuitable for age determination purposes in this study and the technique was subsequently abandoned.

3.3.3 Horn Growth Checks

Although ridges and grooves were visible around the circumference of both bushbuck and duiker horns, these were commonly confined to the basal area. Here, they were often compacted to such an extent that enumeration was not possible, while ridges were rarely visible along the distal portion of the horn where wear was most pronounced. Further, even in those horns where ridges could be counted, it was rarely possible to distinguish between the size or periodicity of these ridges, which varied in number from less than 10 to over 40 in individuals that had been judged, on dental characteristics, to be of similar age. As a result of these limitations, and because assessment of growth checks was highly subjective, the method was considered to have little application as a means of age determination in this study and was consequently rejected.

3.3.4 Allocation of chronological age

Ages were allocated to animals with deciduous dentition by reference to the tooth eruption and replacement sequences of Simpson (1973) and Wilson *et al*. (1984). In most instances, it was not possible to examine the extent to which tooth eruption and replacement times might vary under the prevailing conditions at Weza, because recapture intervals rarely corresponded to those separating specific eruption or replacement times (the decision to recapture animals was primarily influenced by transmitter performance, see Appendix D). Further, most animals were captured or recaptured at night when it was not always possible to determine accurately the extent of tooth eruption (particularly of the molars) and replacement by visual examination. Nevertheless, the state of eruption and replacement of eight subadult bushbuck recaptured at varying intervals, and of one captive animal, showed close agreement (Table 3.4) with the age schedules determined by Simpson (1973).

Longevity records formed the basis of the allocation of chronological ages to the heaviest wear classes of both bushbuck and duiker. Data from captive bushbuck indicate a longevity of 120 to 156 months (Jarvis and Morris 1960; Crandall 1965; Mentis 1972). Although Simpson (1973,1974c) estimated an average longevity for bushbuck of 137 months, the age of the oldest animal he examined (determined by cementum annuli and horn growth checks) was 180 months. A mean age of 156 months was therefore allocated to the bushbuck in this study with the heaviest wear classes.

Records of duiker in captivity suggest a longevity of 108 to 144 months (Flower 1931 cited in Mentis 1972; Jarvis and Morris 1960), but a much older specimen of 258 months, kept under semi-natural conditions, has recently been reported (Wilson *et al*. 1984). The pronounced differential tooth wear of this animal (Wilson *et al*. 1984) was not evident in any of the duiker from Weza and consequently the mean age of 180 months was allocated to the heaviest wear class.

TABLE 3.4 Estimated ages of bushbuck captured as subadults and recaptured at varying intervals.

Bushbuck	INITIAL EXAMINATION		Capture-recapture interval (months)	SECOND EXAMINATION	
	Diagnostic feature of dentition	Estimated age(months) (Table 3.1)		Diagnostic feature of dentition	Estimated age(months) (Table 3.1)
A *	Full milk dentition	1	14,5	2nd molar erupted	14
B	1st molar erupted	7	19	Premolars replacing	26
C	2nd molar erupting	10	14	Premolars replacing	26
D	2nd molar erupted	14	10	Premolars replacing	26
E	2nd molar erupted	14	10	Premolars replacing	26
F	2nd molar erupted	14	16	Permanent dentition	30+
G	3rd molar erupting	19	13	Permanent dentition	30+
H	Premolars replacing	26	6	Permanent dentition	30+
I	Premolars replacing	26	6	Permanent dentition	30+

* - neonate; hand-reared and kept captive for 14,5 months.

A pattern of tooth attrition which follows a negative exponential rate of decay (as described by Spinage 1971, 1973a; Grimsdell 1973 and others) was used to allocate chronological age to the intermediate age classes. In general, the intervals separating two successive wear classes were longer in older bushbuck and duiker (Tables 3.5 and 3.6 respectively), with one notable exception. The pattern of wear on the teeth of the sole representative of duiker Age Class 18 (Fig. 3.12), although distinct, was considered to be only slightly more extensive than the wear visible on the teeth of duiker in Age Class 17 (Fig. 3.11), and consequently these two classes are separated by only 12 months(Table 3.6).

TABLE 3.5 Allocation of chronological ages to adult bushbuck age classes.

Age class	Estimated age (months)
1	48
2	72
3	96
4	132
5	156

TABLE 3.6 Allocation of chronological ages to adult duiker age classes.

Age class	Estimated age (months)
13	36
14	60
15	84
16	120
17	168
18	180

Unfortunately data from recaptured animals were of limited value in the allocation of chronological ages. Thirty one bushbuck were recaptured on a total of 65 occasions, but the time intervals between capture and recapture were not uniform (see Appendix D) and varied from a few weeks to 28 months (Table 3.7). Three duiker were each recaptured once, and one other animal was captured on three occasions, but the average interval between these exercises was less than eight months (range 1-11 months). Furthermore, wear rates could only be determined from those animals where tooth attrition had not progressed from one wear class to the next class during the capture-recapture interval, since it is

TABLE 3.7 Capture-recapture intervals (months) for 31 bushbuck caught on several occasions at Weza.

Bushbuck number	No. of times animal captured						Total interval between 1st & last capture
	2	3	4	5	6	7	
9	4						4
18	18						18
22	7						7
23	2						2
24	15						15
26	13						13
27	14						14
30	19						19
37	5						5
42	1						1
48	7						7
83	6						6
88	6						6
92	2						2
95	5						5
107	8						8
115	7						7
33	0	1					1
36	8	10					18
67	6	3					9
7	4	6	6				16
34	11	3	8				22
41	9	6	0				15
51	8	2	1				11
58	7	4	6				17
65	5	0	10				15
17	6	5	1	1			13
21	10	5	7	6			28
69	0	1	5	5			11
28	5	3	6	5	1	6	26
66	3	3	2	3	3	2	16

the period during which no changes occur (i.e.the time interval between successive age classes) that is of interest. This interval could not be measured precisely from any of the animals examined, although minimum periods where no obvious changes in the pattern of wear occurred were recorded from six bushbuck. Two males (Nos.7 and 24 in Table 3.7) were both assigned ages of 72 months (Age Class 3) when initially captured, and both were again classified as 72 months old when last recaptured 16 and 15 months later respectively. The wear on the teeth of a 96 month old male (No.28) had not differed notably when this animal was allocated the same age 26 moths later, and similarly the chronological age of female No.34 (132 months) was again allocated when she was re-examined after an interval of 22 months (Table 3.7). One of the oldest females examined in this study (No.18) was classified as 156 months old on both occasions when she was captured over a period of 18 months. Finally, no obvious differences were apparent in the heavily worn teeth of an old adult male (No.51) that was captured on five occasions; this animal was allocated a chronological age of 156 months during the 11 months he was studied (Table 3.7).

3.3.5 Eye Lens Mass

3.3.5.1 Bushbuck

Of the 104 pairs of bushbuck lenses that were weighed, 58 (56%) differed by less than 1% of the mean mass of the two lenses, and 97 (93%) differed by less than 5% of the mean. The mean mass calculated for each lens pair was therefore used in all subsequent analyses. There was no significant difference between the dry mass of the left and right eye lenses, and single lenses from 32 additional bushbuck were added to the sample. Differences between male and female mean eye lens mass were not significant and consequently the data from both sexes were combined. Eye lens mass was plotted against chronological age as determined from tooth eruption and replacement or tooth wear(Fig. 3.13).

Initially eye lens growth is fairly rapid, up to approximately 19 months of age, but thereafter is reduced and the variability between individuals of the same age results in considerable overlap between most of the age classes, where for example a mean mass of 0,60g from a pair of lenses could indicate an age of 10 to 156 months (Fig. 3.13).

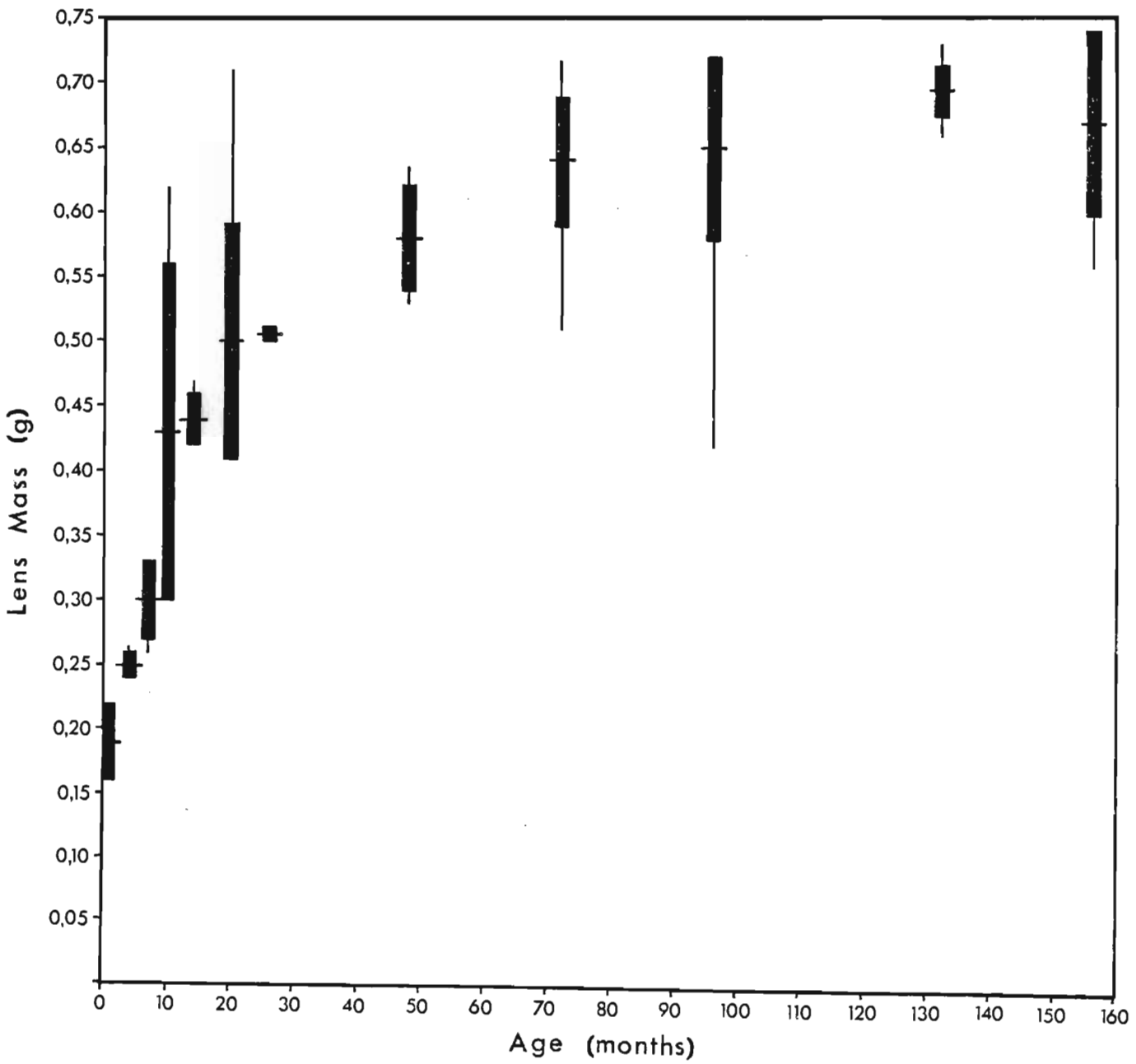


FIGURE 3.13 Growth in mass of dried eye lens with age for male and female bushbuck (range - vertical line; mean - crossbar; standard error - broad portion of line).

3.3.5.2 Duiker

Forty one (45%) of the 92 pairs of duiker lenses differed by less than 1% of the mean calculated for each pair, and 80 (87%) differed from the mean by less than 5%. Differences in the mass of the right and left lenses and between male and female eye lens mass were not significant, and data from both sexes were therefore combined. Single lenses from 14 additional duiker were added to the sample, and eye lens mass was plotted against age (Fig. 3.14).

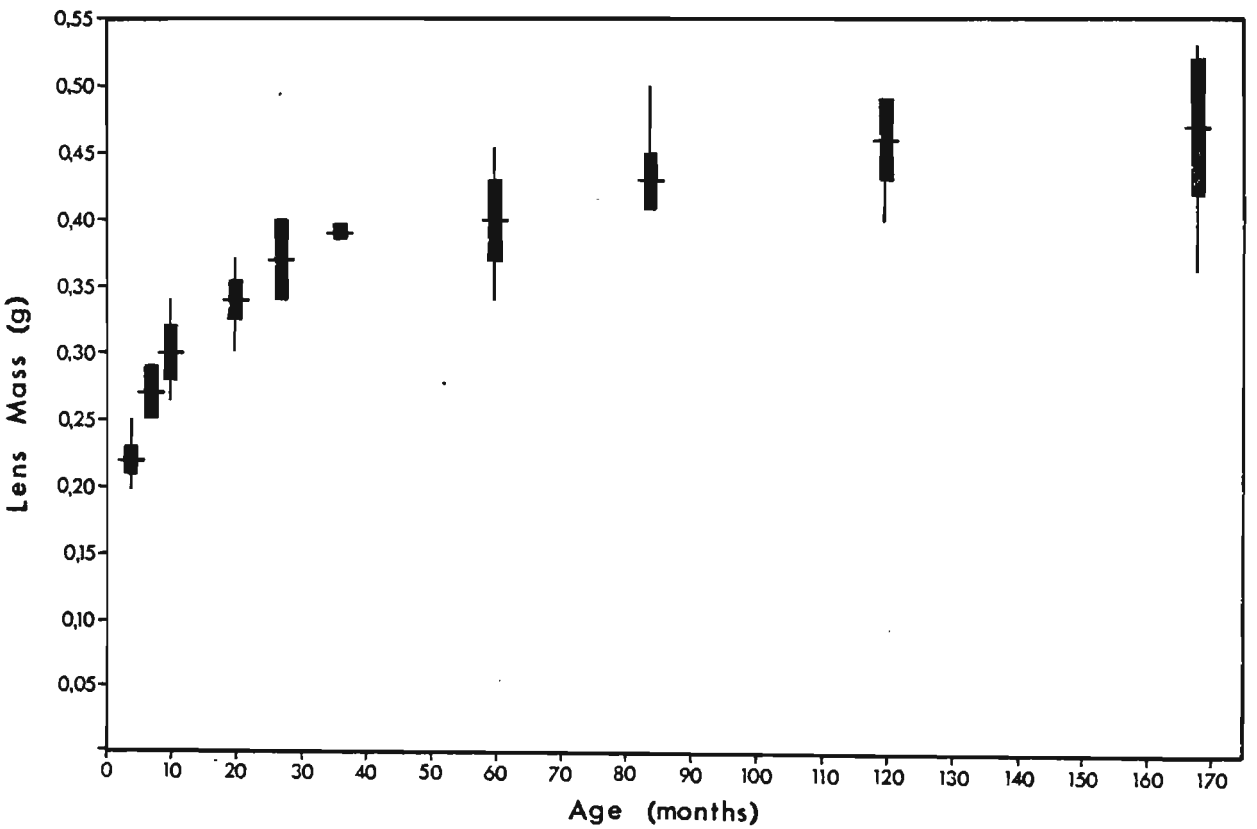


FIGURE 3.14 Growth in mass of dried eye lens with age for male and female duiker (range - vertical line; mean - crossbar; standard error - broad portion of line).

Although less pronounced than in bushbuck, eye lens growth in duiker was most rapid among individuals under 10 months of age. Mean eye lens mass (determined from all the individual values within that age class) increased with age,

but there was extensive individual variation and considerable overlap between the majority of the adult age classes (e.g. 27 months and 168 months, Fig. 3.14).

3.3.6 Field Age Classification

Both bushbuck and duiker are inconspicuous antelope and show strong preferences for habitats with abundant cover. For these reasons, and because of their largely nocturnal, solitary and retiring habits, both species were not easily detected in the field, and prolonged observations could rarely be accomplished. Consequently, the determination of age in the field was often based on brief sightings, and was therefore, on occasion, rather subjective. (See Chapter Ten).

Ages of young and female bushbuck were most readily determined when two or more animals encountered together differed in size. Initially in the study any animal that was considered capable of passing under the stomach of an adult female was classified as an infant, while an animal with a shoulder height less than the mid-shoulder height of an adult female, but larger that an infant was regarded as juvenile. A subadult female was larger than a juvenile but clearly shorter at the shoulder than an adult female. This classification was satisfactory only when animals could be compared to an adjacent adult female. The juvenile category was therefore abandoned, and any female larger than an infant was subsequently classified as either a subadult or an adult. Even with just two female age classes (infants were not sexed), the distinction between infant and subadult, and between subadult and adult was not always obvious, particularly when animals were partially obscured by vegetation or observed over long distances.

Male bushbuck were most easily classified according to horn length and associated changes in pelage. Males observed within 50m could be distinguished from female bushbuck when approximately 14 months of age, when horn growth commences

and the hair on the upper part of the legs begins to darken. This is most noticeable on the insides of the forelegs, where the darkening hair contrasts with the white markings. The hair on the neck and flanks begins to darken when males reach approximately 21 months of age, when horns are approximately the same length as the ears, but the transition to the full dark grey/brown adult coat is not completed until after 30 months of age.

Individuals with horns shorter than the length of the ears (i.e. less than 14cm long) were classified as juveniles, a category which also included animals with no visible horns but with contrasting patterns of dark and light hair on the forelimbs. Males with horns that equalled ear length, but did not exceed one and a half times the length of the ears (i.e. from approximately 14cm to 22cm long) were classified as subadults. Darkening of the hair on the body was most obvious in those subadults with horns approaching 22cm, and these animals were comparable to adult females in body size. Animals with horns longer than one and a half times the length of the ears were classified as adults, and could also be distinguished by their coat colour and larger body dimensions.

Age classification of duiker in the field proved to be much more difficult, and due to their relatively small size, rapid growth rates and lack of sexual dimorphism, it was often impossible even to sex duiker with confidence at a distance. Consequently, although young and female duiker were classified according to the same criteria used for bushbuck (i.e. infant, subadult and adult) when encountered within 50m, nearly 50% of all unmarked duiker sightings were unclassified with regard to sex and age.

The horns of male duiker are relatively short and inconspicuous, rarely extending beyond the length of the ears, and were therefore of less value in field age classification than in bushbuck. Horns are first visible in 4 to 5 month old males and asymptotic horn length is attained before 24 months of age. Males were somewhat subjectively

classified as subadults if horns could be detected and were less than half the length of the ears, and as adults if horn length was closer to ear length. General body dimensions were also considered in such appraisals. The crest of dark hair between the horns, as described by Dorst and Dandelot (1970), Zaloumis and Cross (1974), Hanks (1974), Wynne-Jones (1980) and Smithers (1983) was present only in young males at Weza and had disappeared in males over 24 months of age. Loss of this crest could only be detected when animals were less than 30m away, however, and hence was of limited practical value in field conditions. Females also possess a crest or crown of hair between the ears, and although usually shorter than the crest of subadult males, this could occasionally be mistaken for short horns.

3.3.7 Growth

3.3.7.1 Bushbuck

Growth with age is summarised in Table 3.8, while growth curves for male body mass, body length, girth, shoulder height and horn length are illustrated in Figs. 3.15 to 3.19 respectively. In several instances, the standard errors of specific means extended beyond the theoretical asymptote (Figs. 3.15 to 3.19) and consequently age when asymptotic growth was reached was considered to be attained when the parameter in question was within 2,5% of the Von Bertalanffy equation asymptotic value (Attwell 1977, 1980; Jeffery and Hanks 1981a). In addition, the earliest age at which the parameter was within 5% of the theoretical asymptotic value was also noted for comparative reasons, as detailed in the discussion.

The theoretical Von Bertalanffy growth equations indicate that males were considerably larger than females for all of the growth aspects examined (Table 3.8), and when all of the measurements that fell within 5% of the respective theoretical asymptotes were compared, these differences were highly significant ($p<0,001$) for every parameter measured

TABLE 3.8 Von Bertalanffy equation for growth in age in male and female bushbuck.

Parameter	Sex	Von Bertalanffy equation
Ear Length	M	$l_t = 14{,}06(1-e^{-0{,}145[t+3{,}334]})$ cm
Ear Length	F	$l_t = 12{,}79(1-e^{-0{,}135[t+9{,}969]})$ cm
Shoulder Height	M	$h_t = 83{,}51(1-e^{-0{,}069[t+9{,}105]})$ cm
Shoulder Height	F	$h_t = 73{,}05(1-e^{-0{,}059[t+17{,}642]})$ cm
Hindfoot Length	M	$l_t = 37{,}01(1-e^{-0{,}147[t+3{,}019]})$ cm
Hindfoot Length	F	$l_t = 33{,}31(1-e^{-0{,}118[t+9{,}696]})$ cm
Tail Length	M	$l_t = 20{,}38(1-e^{-0{,}106[t+2{,}809]})$ cm
Tail Length	F	$l_t = 18{,}35(1-e^{-0{,}071[t+10{,}943]})$ cm
Girth	M	$g_t = 85{,}11(1-e^{-0{,}043[t+12{,}969]})$ cm
Girth	F	$g_t = 69{,}02(1-e^{-0{,}079[t+7{,}984]})$ cm
Body Length	M	$l_t = 158{,}59(1-e^{-0{,}062[t+8{,}681]})$ cm
Body Length	F	$l_t = 134{,}24(1-e^{-0{,}074[t+11{,}874]})$ cm
Mass	M	$m_t = 60{,}06(1-e^{-0{,}055[t+9{,}248]})^3$ kg
Mass	F	$m_t = 34{,}73(1-e^{-0{,}092[t+7{,}767]})^3$ kg
Horn Length	M	$l_t = 35{,}40(1-e^{-0{,}051[t-11{,}235]})$ cm

(Table 3.9). Although there was little difference between the sexes in the ages at which shoulder height and hindfoot length asymptotes were attained, asymptotic tail length was attained at a later age in females, while growth in the other examined dimensions was much more prolonged in males (Table 3.10). In addition, the order in the ages at which asymptotic growth for each parameter was attained also differed between the sexes (Table 3.10). In males, asymptotic growth was attained progressively later with age in the order: ear length, hindfoot length, tail length, shoulder height, body length, girth, body mass and horn length (Table 3.10). Horns, however, were only discernible once males were 14 months old (Fig. 3.19).

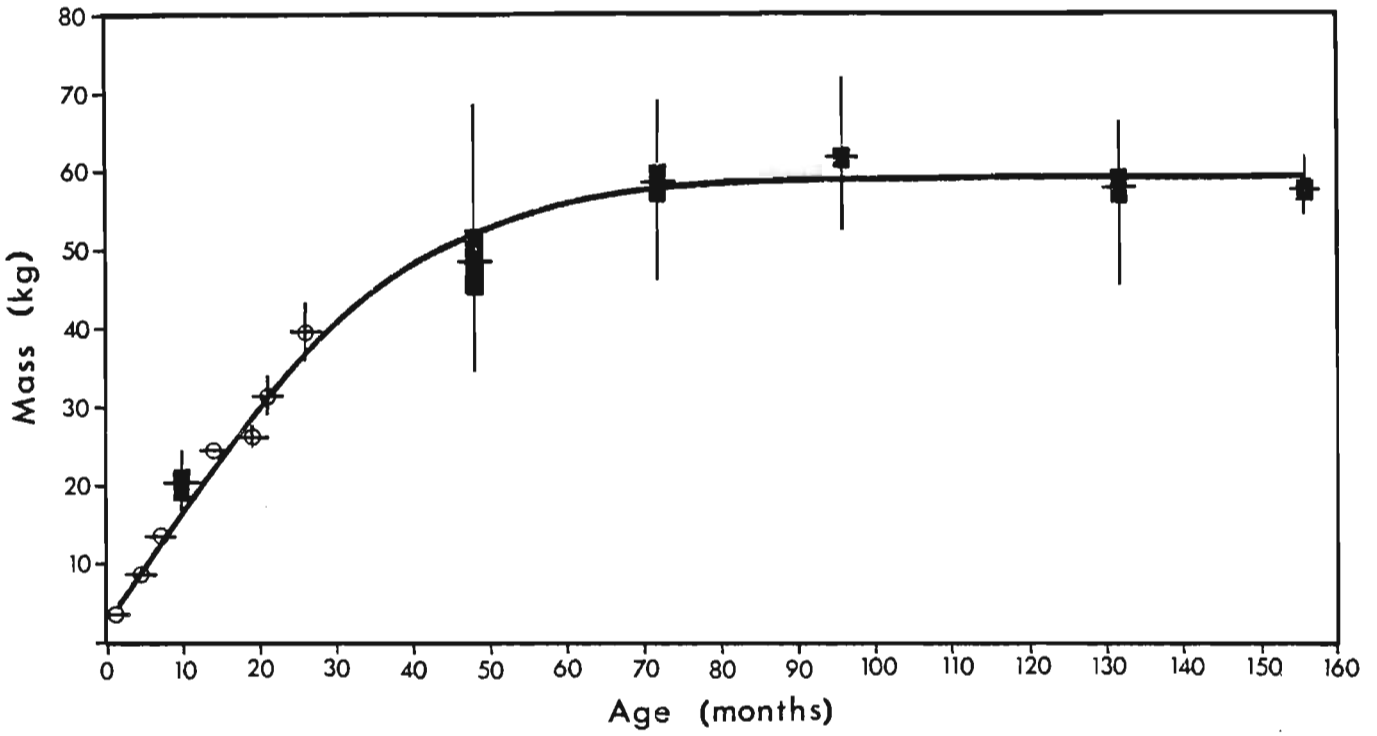


FIGURE 3.15 Theoretical Von Bertalanffy growth curve for body mass in male bushbuck (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.8.

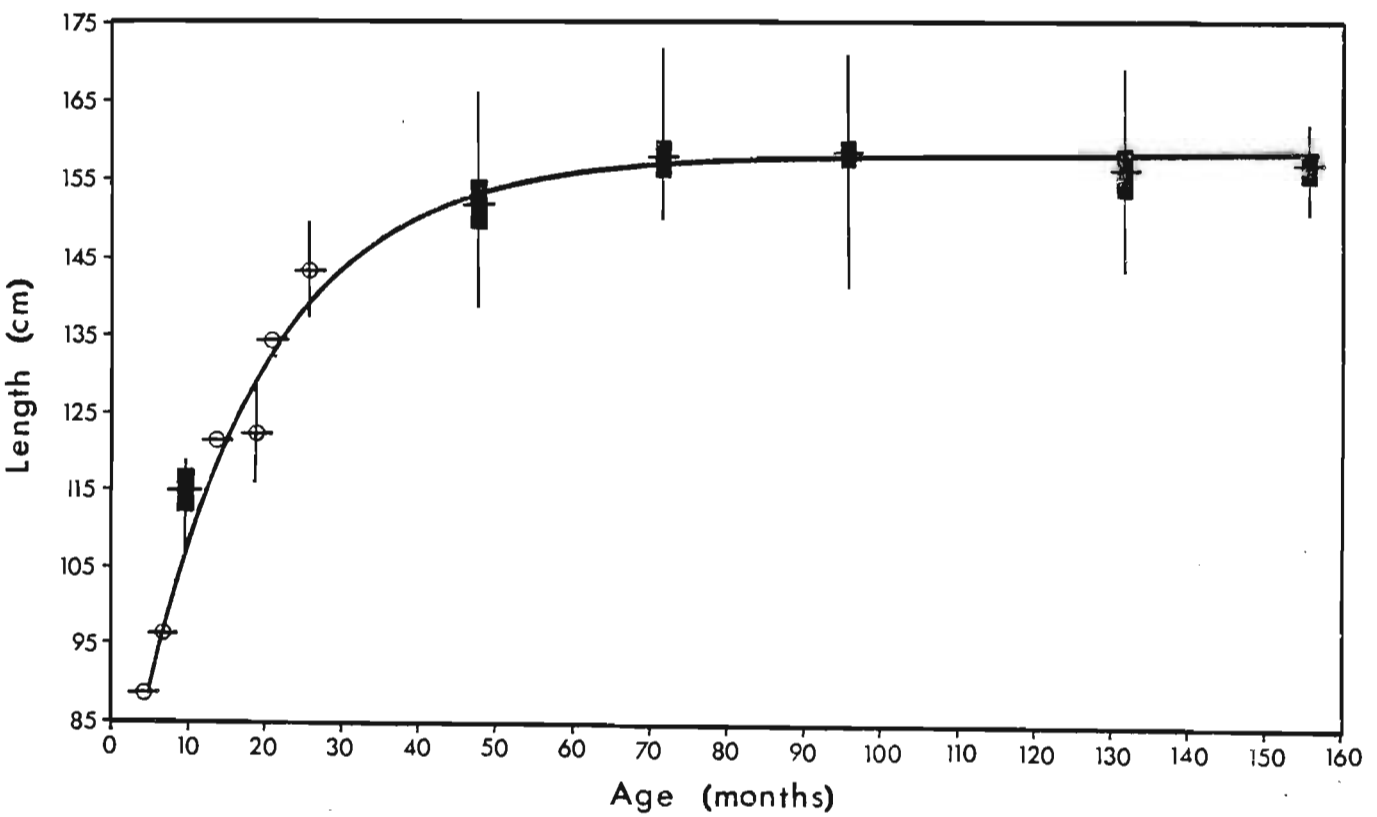


FIGURE 3.16 Theoretical Von Bertalanffy growth curve for body length in male bushbuck (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.8.

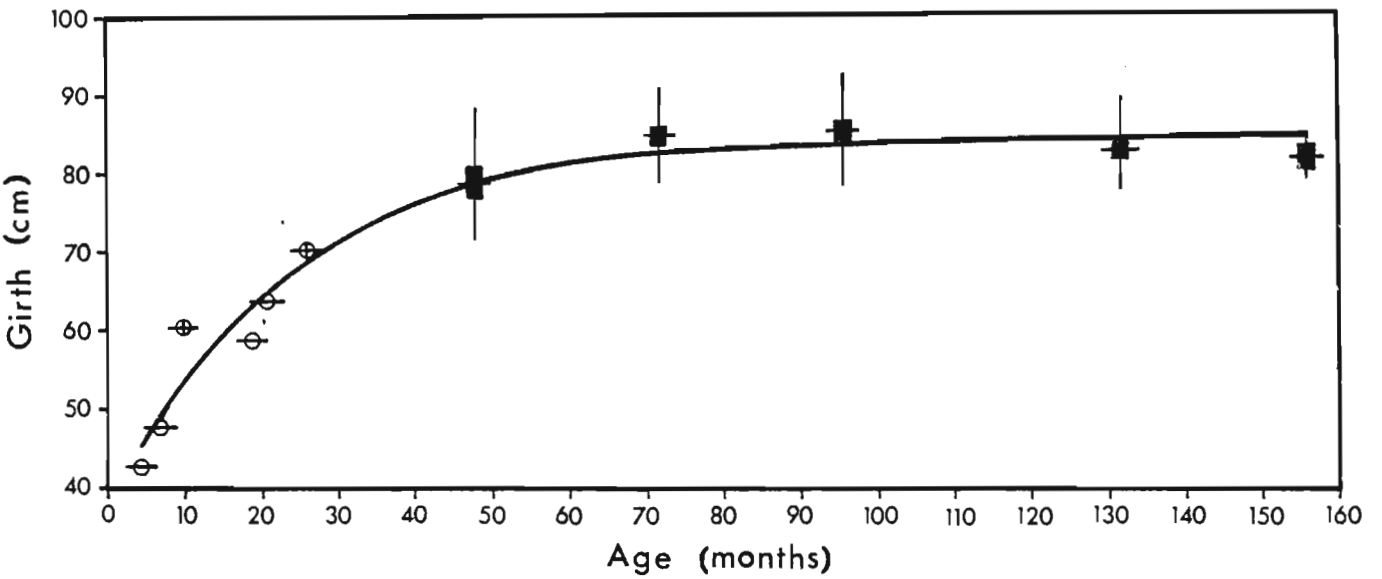


FIGURE 3.17 Theoretical Von Bertalanffy growth curve for girth in male bushbuck (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.8.

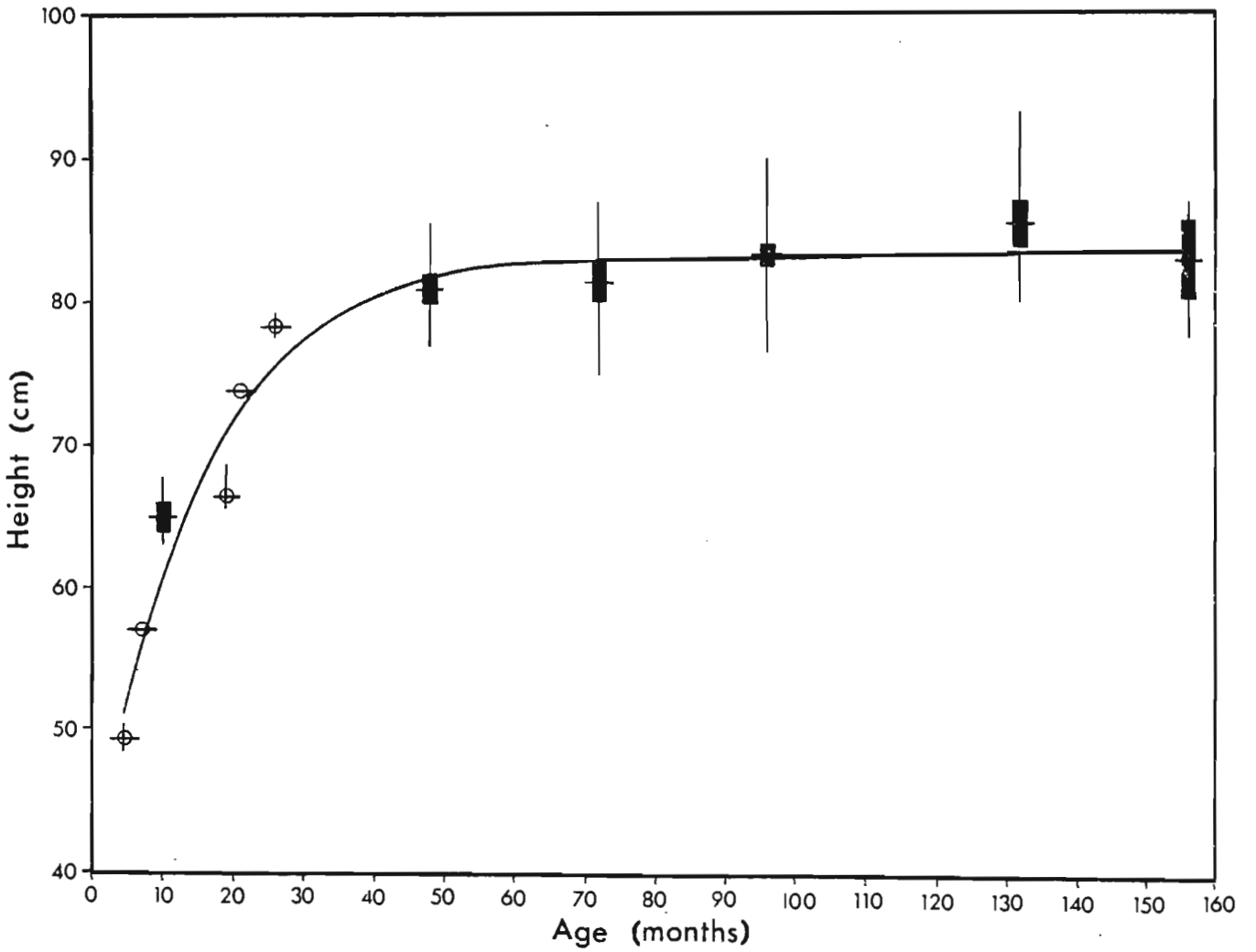


FIGURE 3.18 Theoretical Von Bertalanffy growth curve for shoulder height in male bushbuck (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 -open circle). The equation is presented in Table 3.8

TABLE 3.9 Summary of morphometric data for comparison between sexes of bushbuck at Weza. (Data are derived from those values greater than 95% of the relevant asymptotes).

	Asymptote	Asymptote -5% = Min	Mean	Max.	Sample size	Proportion of culled samples (%)	Difference between means	t value	level of significance
Body Mass (kg)									
Males	60,06	57,1	62,88	71,5	44	54%	26,35	37,68	p< 0,001
Females	34,73	33,0	36,53	44,0	40	53%			
Body length (cm)									
Males	158,59	150,7	159,44	171,9	52	68%	22,95	22,89	p< 0,001
Females	134,24	127,5	136,49	151,0	51	73%			
Girth (cm)									
Males	85,11	80,8	85,42	92,8	46	71%	15,49	24,07	p< 0,001
Females	69,02	65,6	69,93	77,1	39	65%			
Shoulder Height (cm)									
Males	83,51	79,3	84,72	95,6	48	66%	11,39	17,90	p< 0,001
Females	73,05	69,4	73,33	79,8	38	60%			
Hindfoot Length (cm)									
Males	37,01	35,2	37,07	39,7	68	85%	3,73	20,03	p< 0,001
Females	33,31	31,6	33,34	35,9	57	81%			
Tail Length (cm)									
Males	20,38	19,4	21,28	25,2	45	60%	2,41	9,14	p< 0,001
Females	18,35	17,4	18,87	24,4	45	64%			
Ear Length (cm)									
Males	14,06	13,4	14,18	15,2	54	68%	1,20	13,00	p< 0,001
Females	12,79	12,2	12,98	14,4	53	76%			

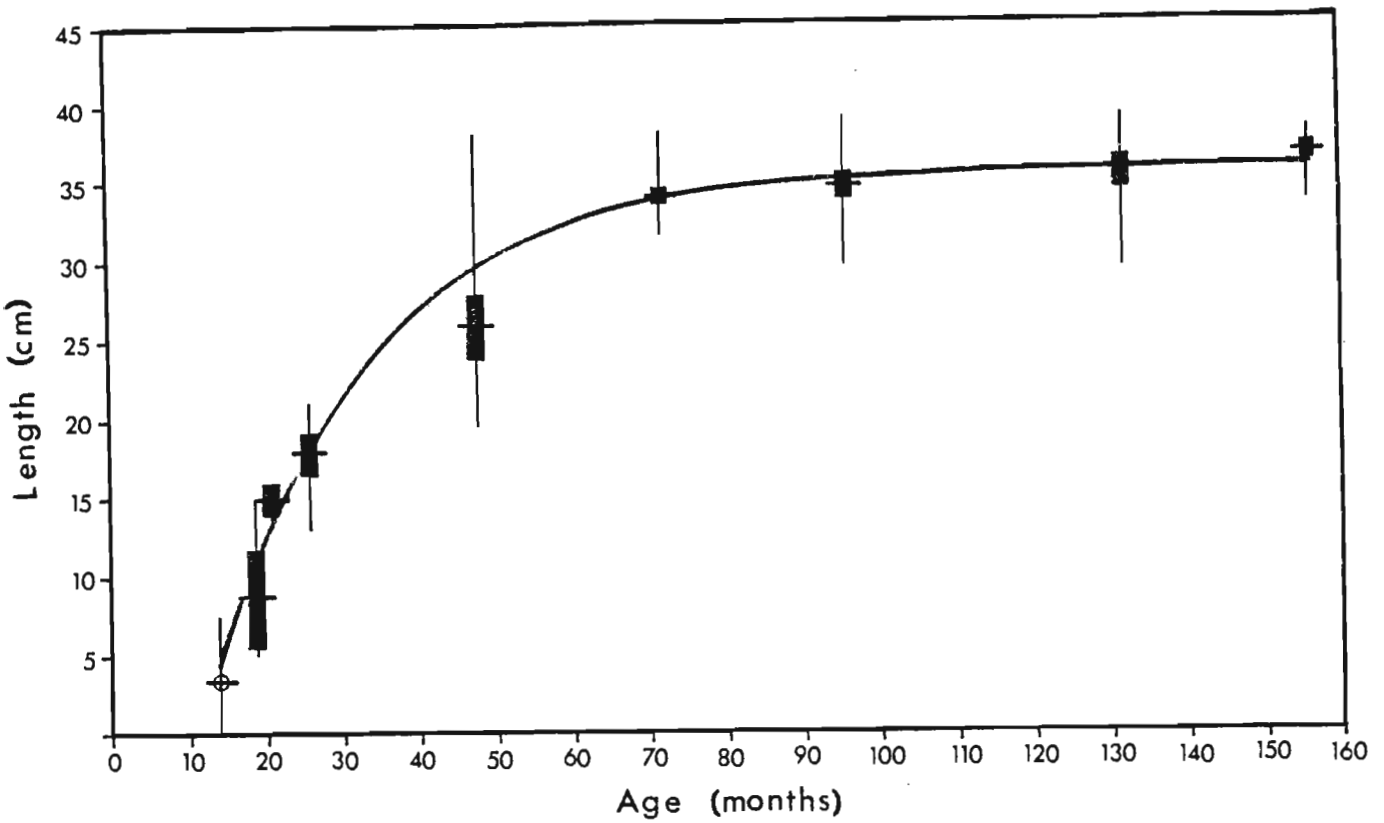


FIGURE 3.19 Theoretical Von Bertalanffy growth curve for horn length in male bushbuck (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.8.

TABLE 3.10 Ages (in months) of attainment of (a) theoretical asymptotic value -5% and (b) theoretical values -2,5% for various body measurements of bushbuck at Weza.

Body measurement	MALES		FEMALES	
	(a) age at asymptotic value -5%	(b) age at asymptotic value-2,5%	(a) age at asymptotic value -5%	(b) age at asymptotic value-2,5%
Ear length	18	22	13	17
Tail length	26	32	32	41
Hindfoot length	18	22	16	22
Shoulder height	34	45	34	45
Girth	57	73	30	39
Body length	40	51	29	38
Body mass	65	78	37	45
Horn length	70	84	-	-

3.3.7.2 Duiker

Duiker growth with age is summarised in Table 3.11 and growth curves for male body mass, body length, girth, shoulder height and horn length are presented in Figs. 3.20 to 3.24 respectively. Comparisons between the sexes reveal that males were significantly smaller ($p<0,001$) than females in body mass, body length and tail length when all of the measurements that fell within 5% of the respective theoretical asymptotes were considered. Differences between the sexes in the mean values of all other parameters, and in the ages at which these are attained, were slight however (Tables 3.12 and 3.13). As for bushbuck, duiker horns which were visible at approximately 4 months of age (Fig. 3.24)

TABLE 3.11 Von Bertalanffy equation for growth in male and female duiker.

Parameter	Sex	Von Bertalanffy equation
Ear Length	M	$l_t = 11,89(1-e^{-0,383[t-0,006]})$ cm
Ear Length	F	$l_t = 11,65(1-e^{-0,567[t-0,237]})$ cm
Shoulder Height	M	$h_t = 56,28(1-e^{-1,506[t-3,449]})$ cm
Shoulder Height	F	$h_t = 56,69(1-e^{-0,374[t+0,685]})$ cm
Hindfoot Length	M	$l_t = 29,03(1-e^{-0,406[t+0,213]})$ cm
Hindfoot Length	F	$l_t = 29,58(1-e^{-0,308[t+2,039]})$ cm
Tail Length	M	$l_t = 11,46(1-e^{-0,839[t-2,818]})$ cm
Tail Length	F	$l_t = 12,28(1-e^{-0,398[t+0,672]})$ cm
Girth	M	$g_t = 51,39(1-e^{-0,339[t-0,705]})$ cm
Girth	F	$g_t = 51,33(1-e^{-0,299[t+0,796]})$ cm
Body Length	M	$l_t = 100,96(1-e^{-0,443[t-1,042]})$ cm
Body Length	F	$l_t = 102,10(1-e^{-0,365[t+0,499]})$ cm
Mass	M	$m_t = 14,25(1-e^{-0,221[t+2,865]})^3$ kg
Mass	F	$m_t = 16,50(1-e^{-0,194[t+3,433]})^3$ kg
Horn Length	M	$l_t = 10,71(1-e^{-0,203[t-4,043]})$ cm

continued growing beyond the age at which all other dimensions had reached their asymptotes (Table 3.13).

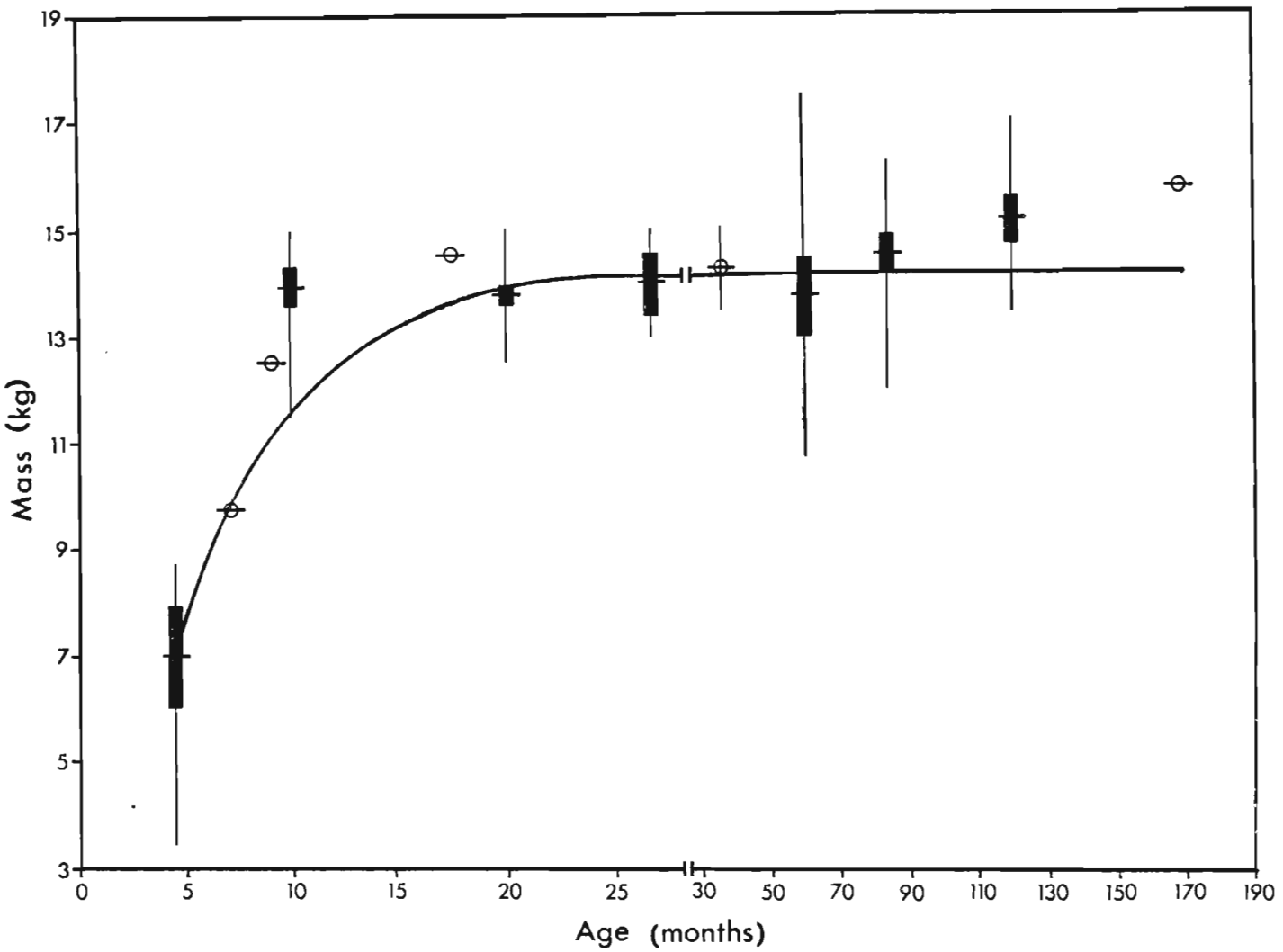


FIGURE 3.20 Theoretical Von Bertalanffy growth curve for body mass in male duiker (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.11.

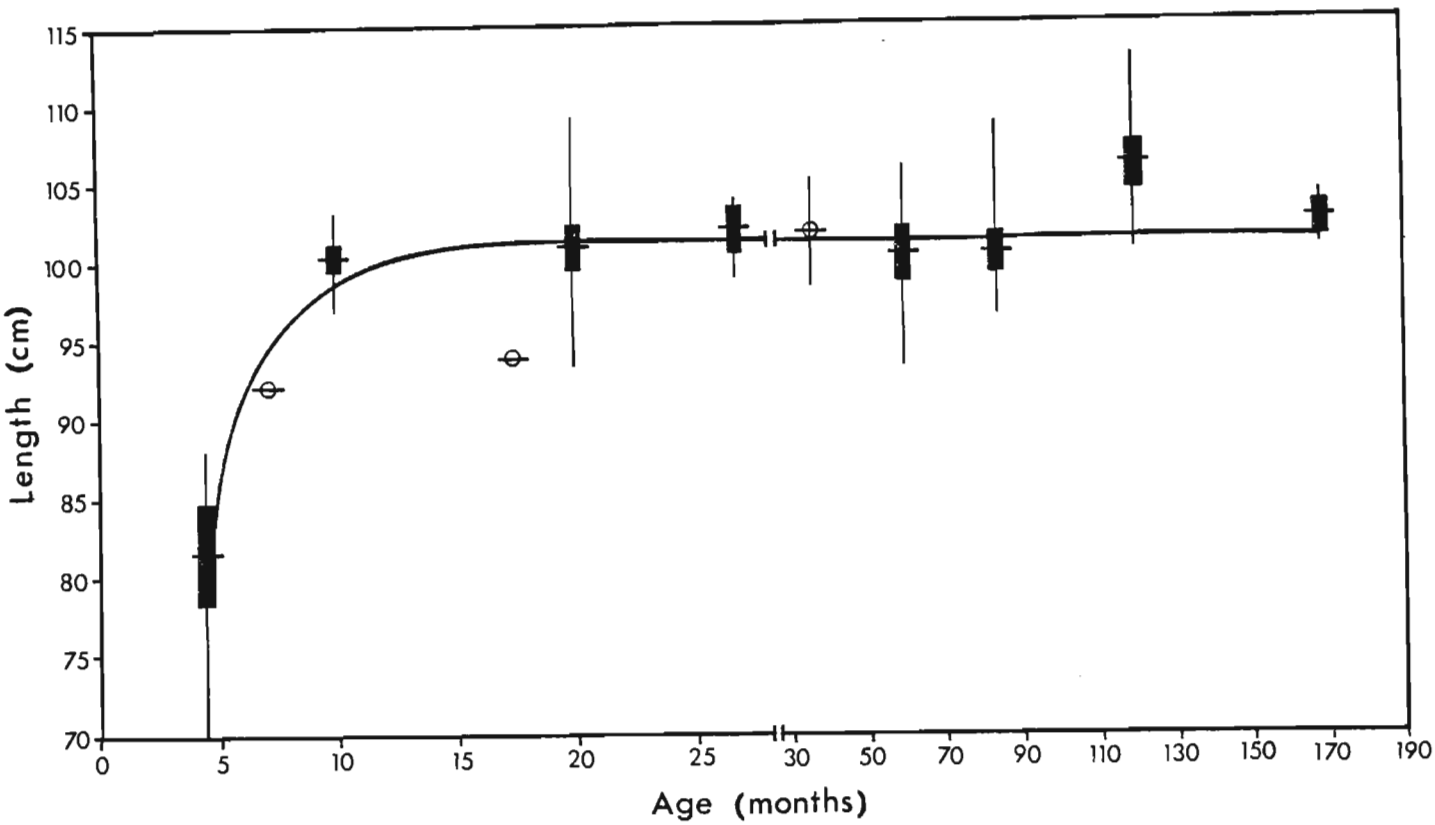


FIGURE 3.21 Theoretical Von Bertalanffy growth curve for body length in male duiker (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.11.

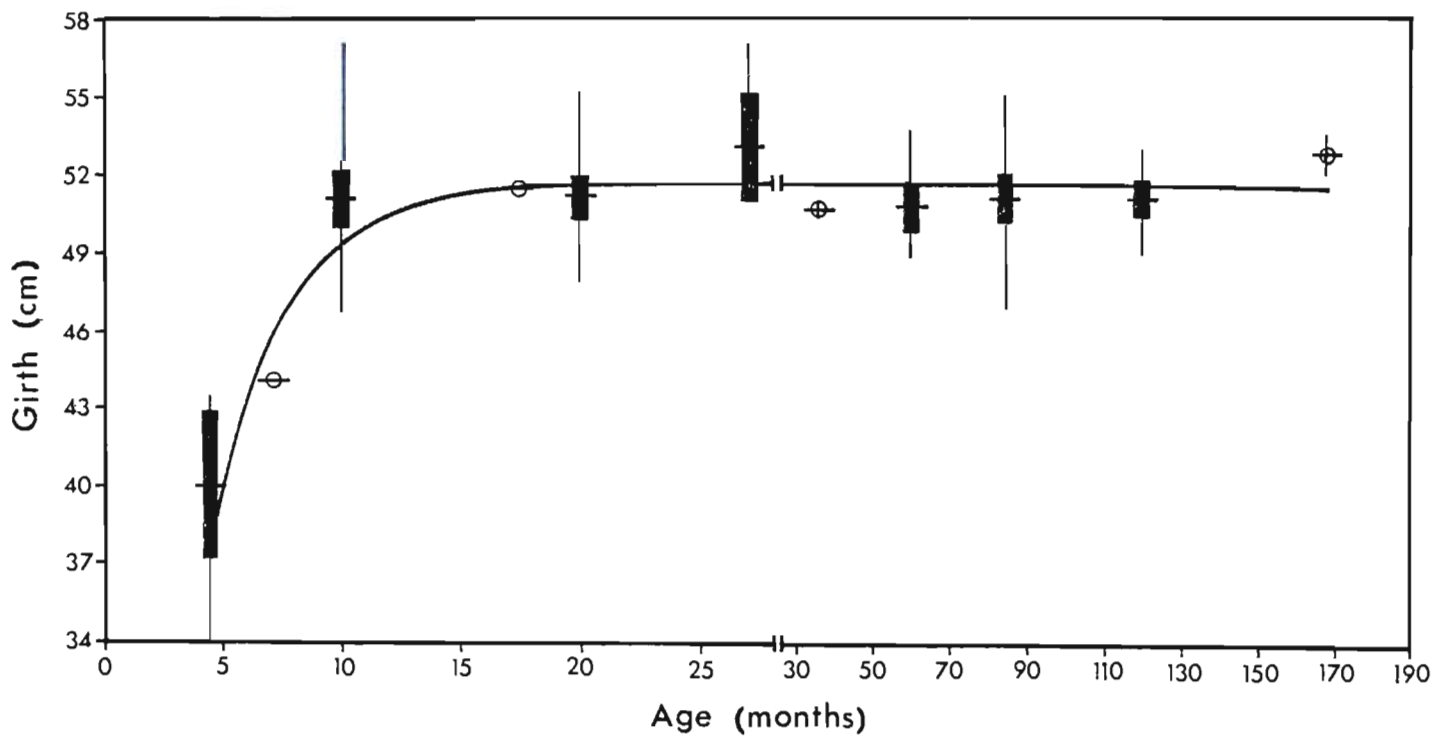


FIGURE 3.22 Theoretical Von Bertalanffy growth curve for girth in male duiker (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.11.

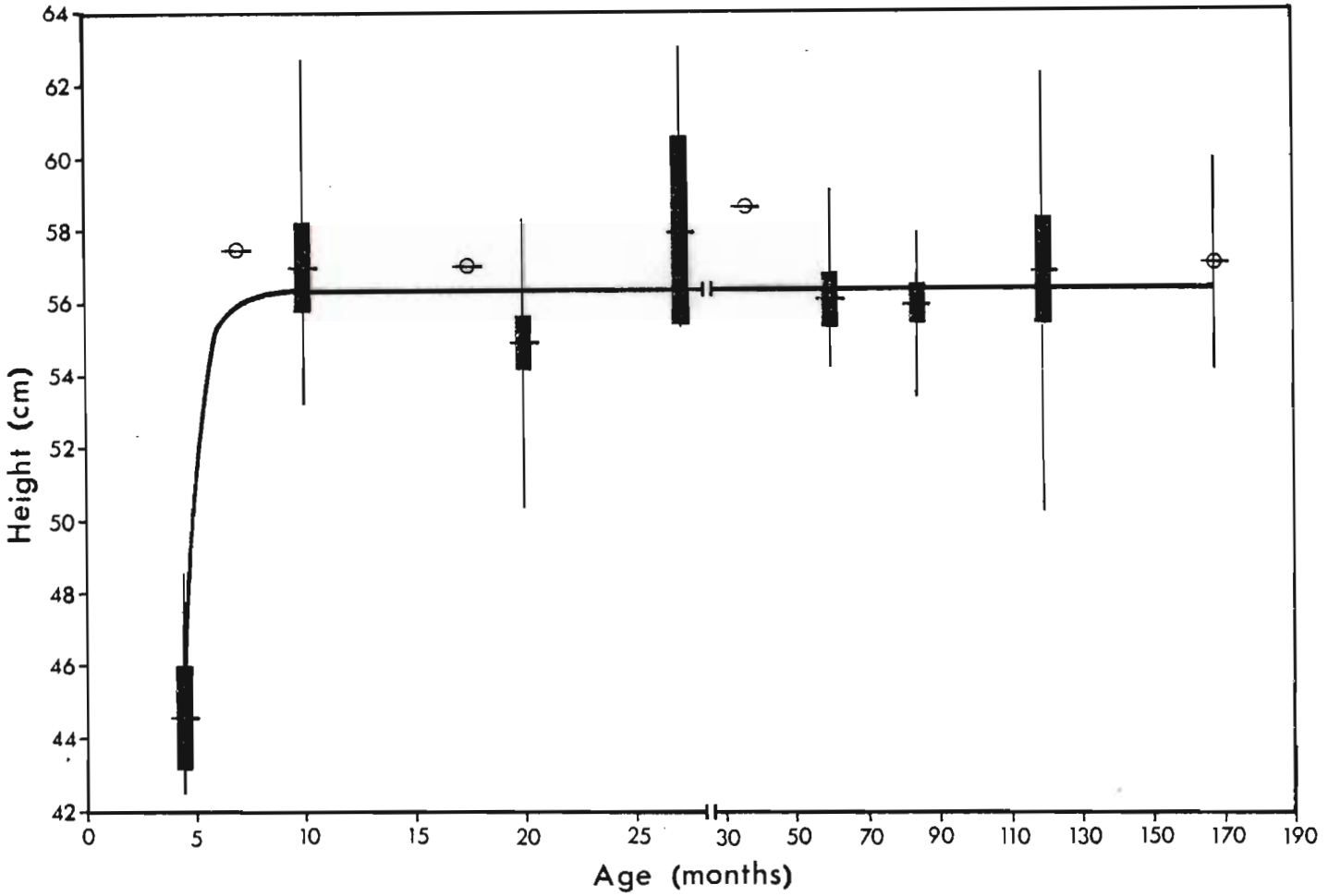


FIGURE 3.23 Theoretical Von Bertalanffy growth curve for shoulder height in male duiker (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.11.

3.3.7.3 Mass estimation

Of the several combinations of body dimensions they measured, Howells and Hanks (1975), Hanks et al. (1976) and Jeffery and Hanks (1981a) found that the isometric relationship between live mass (M) and length × girth^2 (LG^2) provided the most reliable means of mass estimation in impala and eland. Similar predictive equations were formulated in this study, and the relationship between mass and length × girth^2 in male bushbuck is illustrated in Fig. 3.25, where:

$M = 3,81 + 49,13\ LG^2$ ($r = 0,953$; $p<0,001$).

TABLE 3.12 Summary of morphometric data for comparison between sexes of duiker at Weza.
(Data are derived from those values greater than 95% of the relevant asymptotes).

	Asymptote	Asymptote -5% = Min	Mean	Max.	Sample size	Proportion of culled samples (%)	Difference between means	t value	level of significance
Body Mass (kg)									
Males	14,25	13,5	14,59	17,50	49	73%	2,26	9,53	$p < 0,001$
Females	16,50	15,7	16,85	19,0	31	53%			
Body Length (cm)									
Males	100,96	95,9	102,06	113,0	54	83%	2,87	3,39	$p < 0,001$
Females	102,10	97,0	104,93	117,0	42	74%			
Girth (cm)									
Males	51,39	48,8	51,93	59,6	43	83%	0,03	0,06	n.s.
Females	51,33	48,8	51,96	59,5	37	70%			
Shoulder Height (cm)									
Males	56,28	53,5	56,77	63,0	47	81%	0,46	0,93	n.s.
Females	56,69	53,9	57,23	62,0	37	74%			
Hindfoot Length (cm)									
Males	29,03	27,6	29,14	31,5	57	88%	0,20	1,35	n.s.
Females	29,58	28,1	29,34	30,8	45	78%			
Tail Length (cm)									
Males	11,46	10,9	12,11	14,9	45	69%	0,96	4,08	$p < 0,001$
Females	12,28	11,7	13,07	17,2	36	62%			
Ear Length (cm)									
Males	11,89	11,3	12,03	13,2	49	75%	0,14	1,31	n.s.
Females	11,65	11,1	11,89	12,7	43	74%			

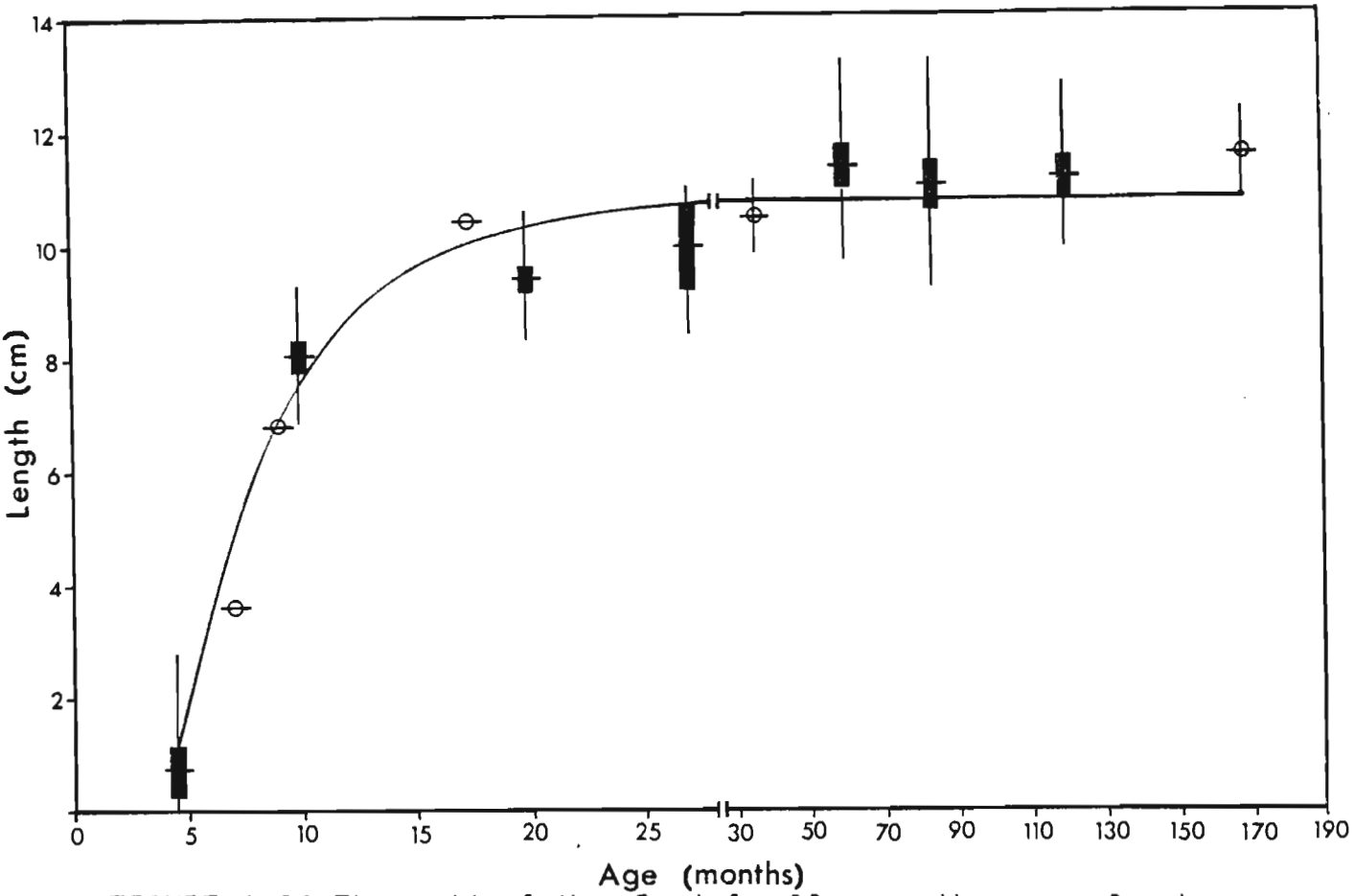


FIGURE 3.24 Theoretical Von Bertalanffy growth curve for horn length in male duiker (range - vertical line; mean - crossbar; standard error - broad portion of line; sample size <3 - open circle). The equation is presented in Table 3.11.

TABLE 3.13 Ages (in months) of attainment of (a) theoretical asymptotic value -5% and (b) theoretical values -2,5% for various body measurements of duiker at Weza.

Body measurement	M A L E S		F E M A L E S	
	(a) age at asymptotic value -5%	(b) age at asymptotic value-2,5%	(a) age at asymptotic value -5%	(b) age at asymptotic value-2,5%
Ear length	8	10	6	7
Tail length	7	8	7	9
Hindfoot length	8	9	8	10
Shoulder height	6	6	8	10
Girth	10	12	10	12
Body length	8	10	8	10
Body mass	16	19	18	20
Horn length	19	23	-	-

The equations for female bushbuck, male duiker and female duiker respectively are:

$M = 2,95 + 48,50\ LG^2$ ($r = 0,909$; $p<0,001$)

$M = 2,71 + 42,72\ LG^2$ ($r = 0,877$; $p<0,001$)

$M = 1,23 + 52,19\ LG^2$ ($r = 0,911$; $p<0,001$)

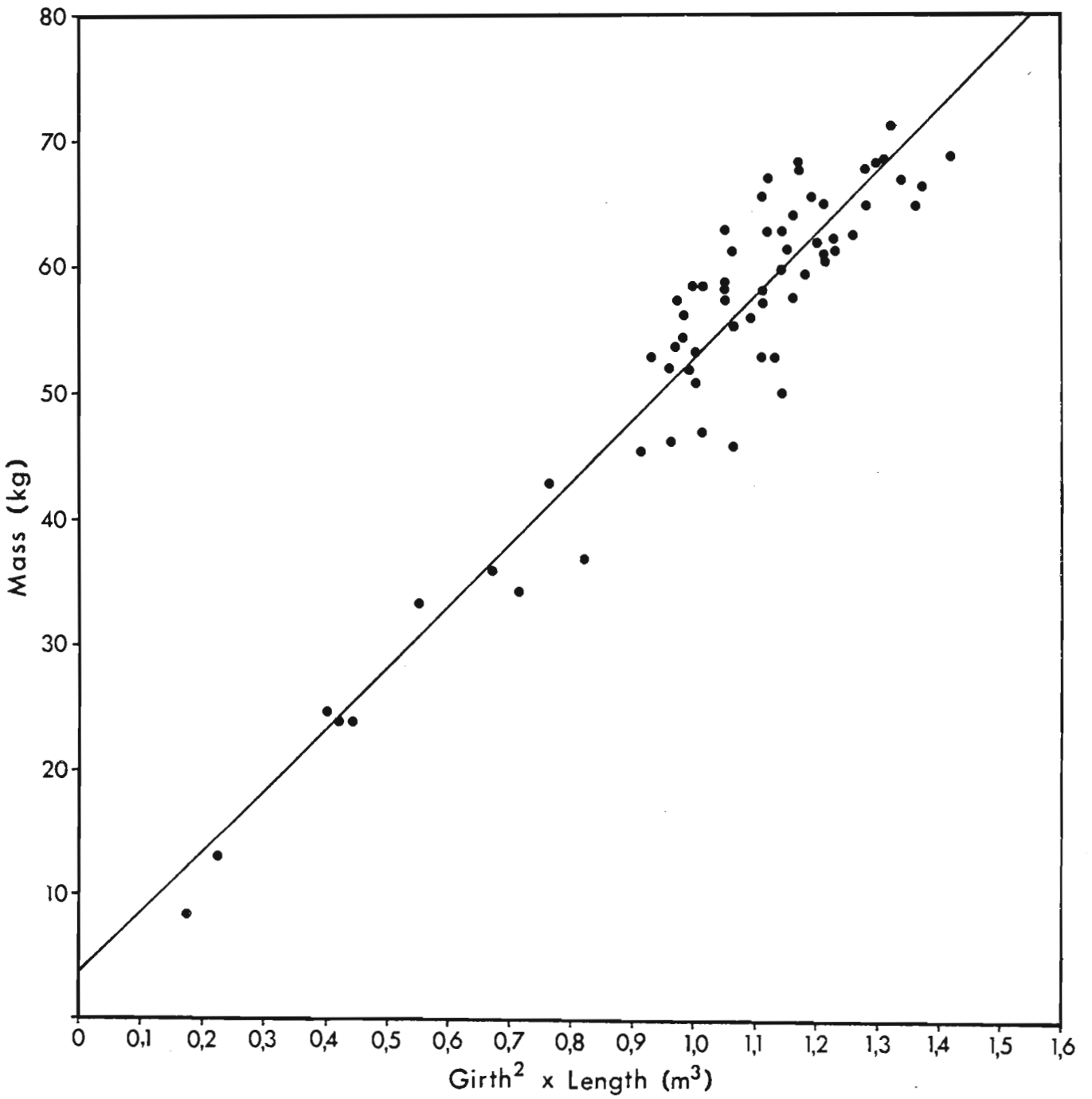


FIGURE 3.25 The relationship between body length x girth^2 and live mass of male bushbuck at Weza. The regression equation is in the text.

3.3.7.4 Carcass mass in relation to live mass

The carcass mass recorded from 25 animals was 79,6% and 81,8% of the live mass in bushbuck and duiker respectively. The relationship between carcass mass (*CM*) and live mass (*LM*) in bushbuck is shown in Fig. 3.26, where the prediction of carcass mass is given by:

$CM = 0,84\ LM - 2,23$ ($r = 0,992$; $p<0,001$)

The relationship between carcass mass and live mass in duiker was almost as good (Fig. 3.27) and equally significant, where:

$CM = 0,86\ LM - 0,49$ ($r = 0,973$; $p<0,001$).

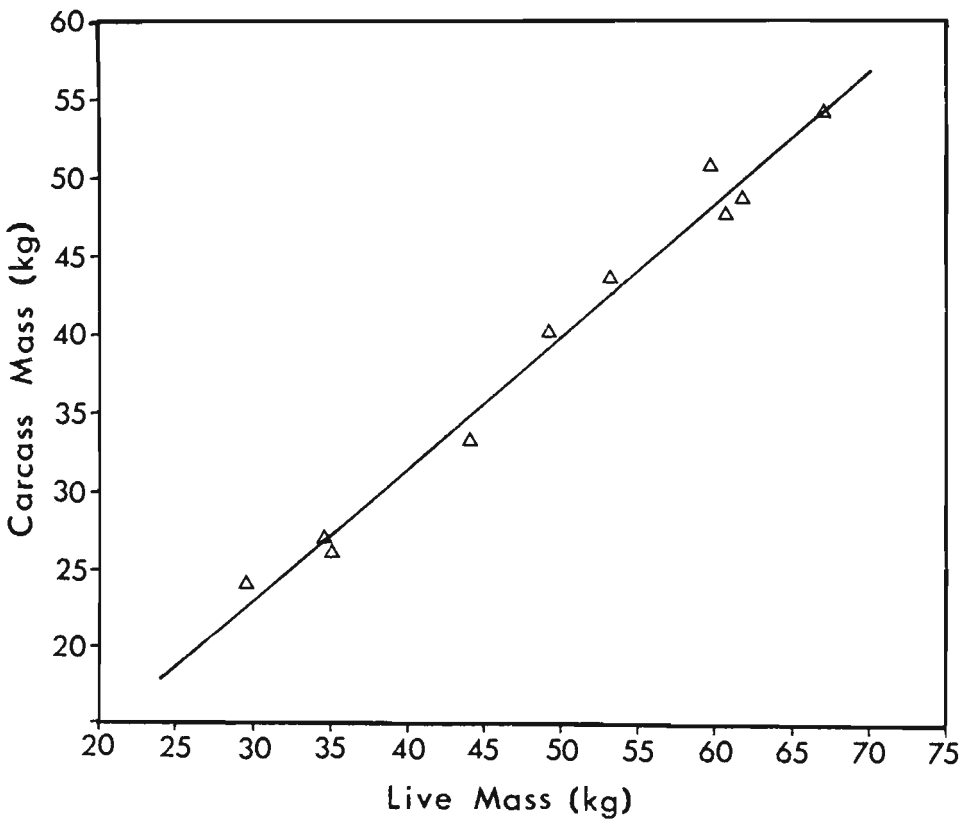


FIGURE 3.26 The relationship between carcass mass and live mass in bushbuck. The regression equation is in the text.

3.3.7.5 Age at maximum productivity

The mean gain in live mass for males and females of both species was calculated at 12 month intervals from the

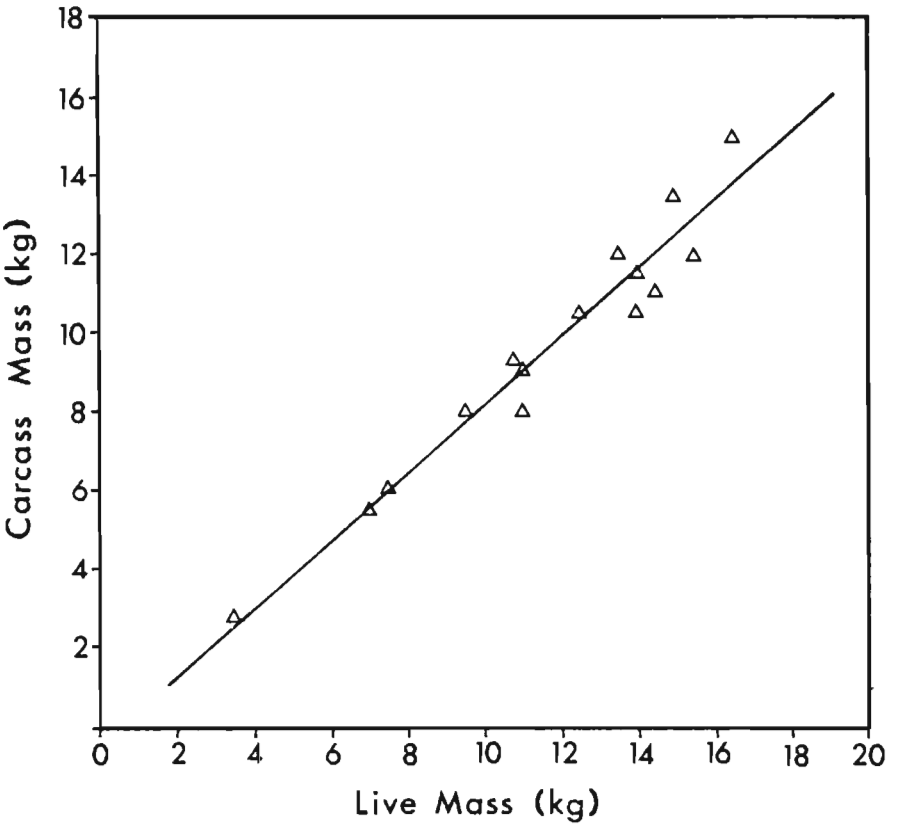


FIGURE 3.27 The relationship between carcass mass and live mass in duiker. The regression equation is in the text.

respective Von Bertalanffy growth equations detailed in Tables 3.8 and 3.11. Mass at birth (see Chapter Five) was subtracted from the theoretical mass attained at 12 months of age; the difference yielded gain in mass during the first year of life, which was subsequently expressed as mean gain (in grammes) per day. Similarly, the theoretical mass at 24 months minus theoretical mass at 12 months provided an estimate of gain in mass during the second year of life. Gain in mass was calculated in 12 month intervals for both sexes until gain was less than 1g/day; these results are summarised in Table 3.14.

In duiker, female gain in mass was slightly higher than in males during the first and second 12 months of life, but pregnant animals were included in both yearly intervals. In both sexes, gain in mass had diminished to a rate of less than 1g/day in duiker over 24 months of age, while maximum productivity clearly occurred during the first 12 months of

life.

Gain in mass during the first 12 months was similar for both male and female bushbuck, but thereafter the rate of gain was considerably higher in males for the next seven successive years. Gain in mass dropped to below 1g/day in females older than 60 months of age, but continued in males until they were 96 months old. Maximum productivity occurred during the first twelve months in female bushbuck, but was maintained for an additional twelve months in males (Table 3.14).

TABLE 3.14 Increase in body mass (g/day) with age.

Age interval (months)	Increase in body mass (g/day)			
	D U I K E R		B U S H B U C K	
	Females	Males	Females	Males
0-11,9	34,3	30,7	46,6	44,6
12-23,9	5,8	3,9	24,7	43,5
24-35,9	<1,0	<1,0	9,6	29,6
36-47,9			3,3	17,4
48-59,9			1,1	9,6
60-71,9			<1,0	5,1
72-83,9				2,7
84-95,9				1,4
96-107,9				<1,0

3.4 DISCUSSION

Although Spinage (1973a) claims that separating degrees of wear, counting cementum lines and the use of other methods are in themselves not difficult, the methods employed during the course of this study, with the exception of tooth eruption and wear, have generally yielded inconclusive and/or highly variable results. The absence of distinct cementum annuli was particularly disappointing, since many other studies, (reviewed in 3.1.3) have shown that these often

provide the most accurate means of age determination and facilitate the allocation of chronological age. Reasons for the lack of clearly defined incremental lines in both bushbuck and duiker are not immediately obvious. Other studies have shown that cementum annuli are most pronounced in those species subjected to environmentally stressful periods, which are usually induced by seasonal variations in climate and/or diet (Mitchell 1963, 1967; Reimers and Nordby 1968; Grimsdell 1973; Miller 1974b; Spinage 1976b; Turner 1977; Jeffery and Hanks 1981b). The cyclical conditions prevailing at Weza, as evident from climatic data (Chapter Two), seasonally significant differences in physiological condition and natural mortality data (Chapter Four), and diet (Chapter Six), would therefore appear to be highly favourable for the formation of cementum annuli, yet these were not obvious in either species. Wilson et al. (1984) considered that the absence of clearly defined annuli in the duiker teeth they examined was primarily due to the relatively constant deposition of cementum resulting from fairly stable conditions of captivity. Thus, while the data from Weza are in agreement as to the poor quality and hence interpretation of cementum annuli in duiker, the results from this study further suggest that the formation of distinct incremental lines in this species is little influenced by fluctuations in environmental conditions. Since annuli have not regularly been detected in a number of other antelope species, including impala (Grafton 1965 cited in Spinage 1973a; Spinage 1971) and reedbuck (Howard 1983), the rate of cementum accretion may, in certain species, be influenced more by genetic than environmental factors.

The presence of cementum annuli have been demonstrated in bushbuck elsewhere (Simpson 1973, 1974c) but the interpretation of their rate of deposition is based on circumstantial evidence and is therefore considered to be highly speculative. Most age determination studies in Africa have shown that the number of cementum annuli deposited each year is related to the pattern of rainfall (Spinage 1973a, 1976b). Thus species inhabiting equatorial regions with a bimodal rainfall tend to produce two cementum lines per

annum, while populations at higher latitudes with a single rainy season exhibit one incremental line each year. Apparent deviations from this pattern have been reported by Simpson and Elder (1969) and Simpson (1973, 1974c) for Kudu and bushbucK respectively. Simpson and Elder (1969) found that two sets of cementum annuli were produced by seasonally breeding Kudu in an area of unimodal rainfall, and therefore they postulated that one set was deposited as a result of nutritional stress, while the other annual cementum line resulted from reproductive stress in both sexes. Supplementary cementum lines associated with reproduction have been reported in a number of temperate cervids, ("rut lines" Low and Cowan 1963; Miller 1974b), but these are often confined to males (Mitchell 1967; Reimers and Nordby 1968). Simpson (1973, 1974c) found a similar pattern of bi-annual lines in bushbucK inhabiting another unimodal rainfall area, but these animals, in contrast to Kudu, bred throughout the year, albeit with two "peaK" birth seasons (see Chapter Five). Simpson (1973, 1974c) made no reference to the possible factors responsible for the bi-annual lines in bushbucK, but merely stated that the rates of cementum deposition "have yet to be substantiated". Further, since no mention was made of any difficulties in interpreting or counting the actual number of lines, these were, presumably, unambiguous. It is difficult to envisage, in a continuously breeding population containing individuals of different reproductive status, how varying levels of reproductively-induced stress could exert a uniform influence on the formation of cementum annuli in both sexes at the same time every year. Thus, although results from this study do not provide an insight into the rate of cementum deposition in bushbucK, it is contended that the relationship between the number of cementum lines and age, as interpreted by Simpson (1973, 1974c) is spurious. As a result, and because his conclusions are somewhat anomalous when compared to the general pattern of cementum layering found elsewhere in Africa, bushbucK from Simpson's study area are considered to be worthy of further examination.

Horn growth checKs provided the only other potential

means of direct age allocation in this study, and it was therefore disappointing to find that these too were totally unsuitable as a practical method for bushbuck and duiker. Horn growth checks were initially proposed as a potential means of age determination in a number of African antelope species by Simpson (1971) who later showed them to be a valid method for the Tragelaphines (Simpson 1972). Subsequent studies have disagreed with this finding, and as in this study, have demonstrated that the method is imprecise and highly subjective (Morris 1973; Anderson 1978). Duiker horn growth checks were even more difficult to interpret, partly because of the size of the horns but also as a result of variable wear. Growth checks are also lost during horn exfoliation, particularly in younger males, thus further limiting the value of this technique. Duiker horn exfoliation has been reported elsewhere (O'Gara and Matson 1975) but was not considered by Simpson (1971).

Since annual increments in cementum and horn could not be assessed, it has only been possible to determine the ages of subadults, using established tooth eruption and replacement schedules, with any degree of confidence. Adults have been classified according to tooth wear criteria and the relative ages assigned to these have, by necessity, been arbitrary. Following Spinage's (1973a, 1979) recommendations however, only the mean age of each class was estimated, not those of individuals.

The criteria used to separate wear classes and the mean relative ages established in this study differ markedly from those of Simpson (1973, 1974c). Differences in wear patterns may, in part, be attributed to genotypic and phenotypic factors (Keiss 1969; Roettcher and Hofmann 1970; Mitchell *et al*. 1977; Wilson *et al*. 1984) particularly since rates of attrition may be significantly influenced by plantation conditions (Habermehl 1961 cited in Roettcher and Hofmann 1970; White 1974). The primary reason for differences in estimated ages between this study and Simpson's (1973) work concerns estimates of longevity, which Simpson estimated from wear criteria and cementum annuli. Arbitrary estimates of

bushbuck and duiker longevity in this study were based on published longevity records in conjunction with cognisance that ages of older animals are often underestimated by tooth wear appraisals (Erickson et al. 1970; Gilbert and Stolt 1970; Spinage 1973a; Thomas and Bandy 1975) and that cementum lines can only provide minimum age estimates due to cementum resorption (Spinage 1967, 1973a; Keiss 1969; Grimsdell 1973) or loss through excessive wear of the cementum pad (Attwell 1977, 1980; Jeffery 1978; Attwell and Jeffery 1981). These phenomena have not been considered in previous tooth wear and/or cementum annuli work in this species (Allsopp 1970; Simpson 1973; Morris 1973).

Ages allocated to the younger wear classes in this study are largely arbitrary, except that reference was made to the recognised pattern of differential tooth wear with age (Spinage 1973a). Since assessment of tooth wear is clearly the most suitable and practical means of age determination in both bushbuck and duiker at Weza, and has been shown to be a valid or superior method for a number of other species (Lowe 1967; Spinage 1971, 1973a, 1976a; Grimsdell 1973; White 1974; Thomas and Bandy 1975), further research should be directed at methods that could provide a more accurate means of age allocation to the classes identified during this study. This could best be achieved by taking regular tooth impressions of marked and recaptured animals over prescribed intervals of time, using repeatable capture methods developed at Weza (Appendix D). As a longer term measure, this practice could be extended to include neonates, which would subsequently become individuals of known-age (Mitchell 1963, 1967; Lowe 1967; Reimers and Nordby 1968; Gasaway et al. 1978; Clutton-Brock et al. 1982a).

For current purposes however, possible errors in the allocation of mean ages to the adult bushbuck and duiker classes are unlikely to have any major bearing on the final conclusions of this study. With the exception of bushbuck growth, relevant biological events requiring a detailed knowledge of age are confined to the subadult classes of both populations (Chapters Four and Five), while other limiting

factors preclude the need for precise ages in analyses of population performance (Chapter Ten). Thus, comparative adult ages are deemed sufficient for all the other principle aspects of this work.

The variability of eye lens mass within each age class and the resultant overlap between the majority of classes (Figs. 3.13 and 3.14) severely limit the value of eye lenses as a complementary or supplementary form of age determination for both bushbuck and duiker. Confidence can only be attached to those values obtained from young individuals where the rate of eye lens growth is fairly rapid, yet as Attwell (1980) points out, the ages of these animals can be determined more accurately and more readily from tooth eruption patterns.

These findings agree with results from previous studies of bushbuck both of which recommended further research. Simpson (1973) suggested that the precision of the method might be enhanced by the collection of a large sample of lenses from one confined area while Morris (1973) considered sex differences in mean eye lens mass to be worthy of further inspection. This study has shown that material from a single geographical source does little to improve the accuracy of the method, and that differences in mean eye lens mass between the sexes are probably influenced by sampling intensity. Non-significant lens mass differences between the sexes in bushbuck and the congeneric greater kudu studied elsewhere, corroborate this view (Simpson and Elder 1968; Simpson 1973, 1974c).

Since eye lenses have been successfully employed in the age determination of numerous small and medium-sized mammals (Longhurst 1964; Friend 1968; Fairall 1969; Morris 1972; Dubock 1979; Perrin 1979), this technique was considered to have high potential for duiker at the onset of this study. Results have demonstrated however, that as in bushbuck, the technique suffers from the same inherent limitations found in many other African and North American species examined, including black-backed jackal Canis mesomelas (Lombaard

1971), warthog Phacochoerus aethiopicus (Child et al. 1965), impala (Fairall 1969; Howells and Hanks 1975), springbok Antidorcas marsupialis (Rautenbach 1971), pronghorn antelope Antilocapra americana (Kolenosky and Miller 1962), white-tailed deer Odocoileus virginianus (Friend 1968), mule deer Odocoileus hemionus (Erickson et al. 1970), black-tailed deer O. hemionus columbianus (Connolly et al. 1963), wildebeest Connochaetes taurinus (Attwell 1977), greater kudu (Simpson and Elder 1968), zebra Equus burchelli (Smuts 1974a), giraffe Giraffa camelopardalis (Hall-Martin 1976), hippopotamus Hippopotamus amphibius (Laws 1968) and elephant Loxodonta africana (Laws 1967). While it may be argued that because eye lens mass is an objective measurement, it is inherently more precise than the subjective technique of visual evaluation of tooth wear (Erickson et al. 1970), the accuracy of the eye lens technique is clearly affected by several sources of variation. These may include natural sources such as disparities in growth, stress (Myers and Gilbert 1968), and the influence of nutrition (Morris 1972) or introduced variation caused by differing fixation and drying times etc. (Friend 1968). Inherent sources of variation are impossible to control, while attempts to reduce introduced variation by standardising methods (e.g. fixation times) may require such exacting procedures as to render the method impractical.

Several authors have concluded that, at best, the lens technique confirms the validity of other age determination criteria employed in their studies (Laws 1967; Smuts 1974a; Hall-Martin 1976; Howells and Hanks 1975). Similar conclusions can be drawn from this study, where mean eye lens mass generally increases with age estimated from tooth wear criteria. However, in the absence of known-age material, both mean eye lens mass and tooth wear are dependent variables, and as such, assurances based on their relationship may be spurious (Dapson 1980). As a result of all of these limitations, and without access to material of known-age, it must be concluded that little can be gained by persisting with eye lens mass in future age determination studies of these two species.

Results from Weza substantiate the findings of Simpson (1973, 1974c) and Morris (1973) in that they clearly demonstrate the sexually dimorphic nature of growth in all the parameters examined for bushbuck older than one year (Tables 3.8 and 3.9). These data further illustrate that growth is generally much more prolonged in males (Table 3.10) and confirm the conclusion by Morris (1973) that male growth in body mass continues throughout life. Because of differing methods of age allocation in adults, independent methods of growth assessment (not specified by Simpson 1973), and the omission of growth equations and ages at which asymptotes were attained (Morris 1973), it is not possible to compare the growth rate of the Weza population with those from Botswana and Zimbabwe. Using identical age criteria to Simpson (1973) for subadults however, it is evident that horn growth is initiated at a later age at Weza (i.e. at 14 months, ten months later than the Botswana population), and more closely resembles horn development recorded from captive animals in Europe (Allsopp 1970). Whether these differences in initial horn growth result from varying levels of nutrition, as has been reported for antler growth in cervids (Roseberry and Klimstra 1975; Mitchell *et al.* 1976), is not known.

Morphometric data from bushbuck at Weza and from other populations are summarised in Tables 3.15 and 3.16 for males and females respectively. Caution should be exercised in comparisons of body size however, because the methods used to derive mean values, where detailed, differ between authors (e.g. body measurements recorded "over the curves" or "between pegs" (Ansell 1965), the inclusion/exclusion of pregnant females, and varying definitions of "adult" animals). Mean data from Weza are derived only from those values that fell within 5% of the relevant asymptotes, and are therefore probably from older animals than those classified elsewhere by dental criteria alone. Further, the absence of raw data from other studies prevents the statistical treatment of differences between these populations. Nevertheless, the two populations of *T.s.*

TABLE 3.15 Comparison between subspecies of mean values for adult body mass and measurements of male bushbuck.

	T.s. ornatus Zambia (Wilson & Child 1964)	T.s. ornatus Zambia (Wilson 1968)	T.s. ornatus Botswana (Smithers 1971)	T.s. ornatus Zimbabwe (Simpson 1973)	T.s ornatus Zimbabwe (Morris 1973)	T.s. sylvaticus Southern Cape (Odendaal 1977)	T.s.sylvaticus Natal (This Study)
ean Body mass (kg)	42,0	42,6	43,1	45,1	49,4	61,7	62,9
	11	7	1	51	8	11	44
ange	29,0-54,0	33,6-55,8	-	-	-	50,0-71,0	57,1-71,5
ean Body Length (cm)	148,0	-	-	-	151,3	154,5	159,4
	8	-	-	-	12	11	52
ange	136,0-166,0	-	-	-	-	135,0-168,0	150,7-171,9
ean Shoulder height (cm)	70,0	-	-	83,2	76,8	84,7	84,7
	8	-	-	2	8	11	48
ange	64,0-74,0	-	-	80,0-86,4	-	76,0-94,0	79,3-95,6
ean Girth (cm)	-	-	-	-	79,2	88,5	85,4
	-	-	-	-	8	11	46
ange	-	-	-	-	-	81,0-96,0	80,8-92,8
ean Hindfoot Length (cm)	-	-	37,6	36,9	36,4	32,7	37,1
	-	-	1	2	13	11	68
ange	-	-	-	36,9-37,0	-	28,5-37,0	35,2-39,7
ean Ear Length (cm)	13,5	-	16,0	14,6	14,5	15,8	14,2
	8	-	1	3	12	11	54
nge	12,1-15,2	-	-	14,0-15,0	-	14,5-18,0	13,4-15,2
an Tail Length (cm)	21,0	-	20,5	-	22,3	21,0	21,3
	8	-	1	-	12	2	45
nge	19,0-24,0	-	-	-	-	20,0-22,0	19,4-25,2

TABLE 3.16 Comparison between subspecies of mean values for adult body mass and measurements of female bushbuck.

	T.s. ornatus Zambia (Wilson & Child 1964)	T.s. ornatus Zambia (Wilson 1968)	T.s. ornatus Botswana (Smithers 1971)	T.s. ornatus Zimbabwe (Simpson 1973)	T.s. ornatus Zimbabwe (Morris 1973)	T.s. sylvaticus Natal (This Study)
Mean Body Mass (kg)	28,0	28,6*	31,9	30,4	31,4	36,5
n	16	8	4	68	11	40
Range	24,0-34,0	22,7-32,2	29,5-36,3	-	-	33,0-44,0
Mean Body Length (cm)	140,0	-	-	-	138,1	136,5
n	13	-	-	-	5	51
Range	133,0-154,0	-	-	-	-	127,5-151,0
Mean Shoulder Height(cm)	64,0	-	-	72,6	68,4	73,3
n	13	-	-	5	11	38
Range	61,0-67,0	-	-	66,5-76,0	-	69,4-79,8
Mean Girth (cm)	-	-	-	-	69,6	69,9
n	-	-	-	-	5	39
Range	-	-	-	-	-	65,6-77,1
Mean Hindfoot Length(cm)	-	-	35,0	33,6	33,7	33,3
n	-	-	3	5	5	57
Range	-	-	32,9-36,2	32,0-35,5	-	31,6-35,9
Mean Ear Length (cm)	13,6	-	13,9	13,9	14,1	12,9
n	13	-	3	9	8	53
Range	12,7-15,2	-	13,5-14,3	13,2-15,0	-	12,2-14,4
Mean Tail Length (cm)	20,0	-	21,2	-	20,3	18,9
n	13	-	3	-	8	45
Range	19,0-22,0	-	20,0-22,5	-	-	17,4-24,4

* Not pregnant

sylvaticus show close agreement in male body mass and size, and are considerably heavier (from 20-33%) and larger than the subspecies T.s. ornatus. Differences between females are generally less pronounced, but are probably significant for body mass, where females at Weza are approximately 13-20% heavier than females of the subspecies T.s. ornatus. These data support Odendaal's (1977) inference that bushbuck at the southern limits of their distribution are heavier and larger than those towards the central portion of their range. Such differences should be taken into consideration when calculating biomass values in these regions.

Previous studies of growth in duiker have demonstrated that females are generally (Wilson and Clarke 1962) or significantly (Wilson et al. 1984) larger than males. The latter authors found body mass to be the only parameter where differences between the sexes were not significant, but they did not detail the reproductive status of their females. Body mass was one of three parameters where females were significantly larger than males in this study, and since only 3 (10%) of the females in the Weza sample were not pregnant, these results support the suggestion of Wilson and Clarke (1962) that sex differences in body mass may be a consequence of pregnancy. With the exception of body length and tail length, (where females were significantly larger, Table 3.10) and in contrast to Wilson et al. (1984), males and females were of almost identical size in all other parameters examined at Weza.

As asymptotic growth is attained at such an early age in duiker (while molariform tooth eruption and replacement is still in progress), rates of growth in both this study and that of Wilson et al. (1984) are based on the same age determination criteria, and could therefore be directly compared.

Differences in the ages at which asymptotic growth was attained were so great however, with duiker from Weza consistently showing faster growth rates and reaching asymptotic growth up to 16 months earlier, that they

warranted further examination. Wilson et al. (1984) did not detail how asymptotic age was determined in their study, but by substituting each of their asymptotic ages into the respective Von Bertalanffy equations for each parameter they examined, the solved equations revealed that different methods of assessing asymptotic age had been used in these two studies. In this current study, asymptotic age was taken as the earliest age at which the solved equation fell within 5% of the true asymptote. Using the data from Wilson et al. (1984), their ages provided values that fell within a range of 2-8% of their true asymptotes, and consequently are not comparable. For example, Wilson et al. (1984) suggested that duiker exhibit sexual dimorphism in rates of growth, since males reached asymptotic mass and shoulder height at 22 months, 6 months later than females. No appreciable differences were evident in rates of growth in males and females in this study, and if their data for shoulder height are analysed in a similar manner to that used for the duiker at Weza, both males and females attain asymptotic shoulder height (i.e. within 5% of the true asymptote) at precisely the same age of 16 months.

When the data of Wilson et al. (1984) were treated in an identical manner to this study, comparisons between the two populations revealed that asymptotic growth is still attained at a much earlier age in duiker from Weza (e.g. asymptotic shoulder height in males attained 10 months earlier). With the exception of body mass and horn growth, both sexes attain full growth within their first year at Weza. Possible reasons for these different rates of growth may be related to population density or overt modifications in the quality and/or quantity of available habitat as discussed in Chapter Ten.

Summaries of mean values of body mass and measurements from different populations of duiker (none identified to subspecies) are presented in Tables 3.17 and 3.18 for males and females respectively. Although the cautionary note regarding direct comparisons of body size between populations mentioned above is equally applicable here, it is apparent

TABLE 3.17 Comparison between mean values for adult body mass and measurements of male duiker.

	Zambia Wilson (1968)	Botswana Smithers (1971)	Zambia Wilson & Clarke (1962)	Natal Schmidt (1984a)	Transvaal Rautenbach (1982)	Natal This Study
Mean Body Mass (Kg)	13,8	18,7	12,9	16,2	16,3	14,6
n	172	24	82	2	2	49
Range	12,7-16,6	15,3-21,2	9,0-17,0	16,1-16,2	-	13,5-17,5
Mean Body Length (cm)	-	109,7	95,0	103,6	102,6	102,1
n	-	23	23	2	3	54
Range	-	103,0-116,0	83,0-103,0	-	95,5-112,5	95,9-113,0
Mean Shoulder Height (cm)	-	-	50,0	61,3	-	56,8
n	-	-	23	2	-	47
Range	-	-	46,0-53,0	59,6-63,0	-	53,5-63,0
Mean Girth (cm)	-	-	-	55,3	-	51,9
n	-	-	-	2	-	43
Range	-	-	-	54,5-56,0	-	48,9-59,7
Mean Hindfoot Length (cm)	-	32,6	25,0	30,4	30,0	29,1
n	-	25	23	2	3	57
Range	-	29,0-34,9	23,0-27,0	29,8-30,9	29,0-32,0	27,6-31,5
Mean Ear Length (cm)	-	12,9	11,5	11,8	11,7	12,0
n	-	24	23	2	3	49
Range	-	11,5-14,8	10,0-12,0	11,5-12,0	11,0-12,5	11,3-13,2
Mean Tail Length (cm)	-	12,9	11,0	11,2	10,6	12,1
n	-	23	23	2	3	45
Range	-	10,5-16,0	8,5-13,0	11,0-11,3	10,5-10,7	10,9-14,9

TABLE 3.18 Comparison between mean values for adult body mass and measurements of female duiker.

	Zambia Wilson (1968)	Botswana Smithers (1971)	Zambia Wilson & Clark (1962)	Natal Schmidt (1984a)	Transvaal Rautenbach (1982)	Natal This Study
Mean Body Mass (Kg)	14,1	20,7	13,7	16,7	15,9	16,9
n	81	37	85	4	4	31
Range	12,7-16,8*	17,1-25,4	9,0-20,0	15,3-18,5	10,0-20,0	15,3-19,0
Mean Body Length (cm)	-	113,5	101,0	106,4	107,7	104,9
n	-	37	17	4	5	42
Range	-	105,0-125,0	93,1-111,0	103,7-112,2	108,0-110,0	97,0-117,0
Mean Shoulder Height (cm)	-	-	52,0	57,1	-	57,2
n	-	-	17	4	-	37
Range	-	-	46,0-56,0	54,0-61,0	-	53,9-62,0
Mean Girth (cm)	-	-	-	52,4	-	51,9
n	-	-	-	4	-	37
Range	-	-	-	50,8-53,5	-	48,8-59,5
Mean Hindfoot Length (cm)	-	32,7	25,0	29,6	29,8	29,3
n	-	38	17	4	5	45
Range	-	24,5-35,5	23,0-27,0	29,1-30,4	28,5-32,0	28,1-30,8
Mean Ear Length (cm)	-	12,9	11,5	11,0	12,7	11,9
n	-	37	17	4	5	43
Range	-	11,8-14,5	10,0-12,0	10,2-11,4	11,5-14,6	11,1-12,7
Mean Tail Length (cm)	-	15,0	12,0	11,5	11,1	13,1
n	-	36	17	4	5	36
Range	-	12,2-19,5	10,5-14,0	10,5-12,3	10,5-11,3	11,7-17,2

* Not pregnant

that duiker exhibit considerable variation in size throughout their southern African range. This was not fully appreciated by Schmidt (1984a) who compared duiker from Zambia (using data from Wilson and Clarke 1962) with another subspecies from Natal. He found that the latter population was significantly heavier and larger, but also had significantly shorter ears and tails, than duiker from Zambia, and concluded that these two populations illustrated Bergmann's and Allen's rules. Unfortunately, his data from Natal were based on an extremely small sample size of two adult males and four adult females, while methods and scales of measurement, and the proportions of pregnant females also differed between these two samples. Even if these differences in body size do in fact illustrate Bergmann's and Allen's rules, this trend is not evident throughout southern Africa, because the largest and heaviest duiker recorded to date come from Botswana, and these are appreciably larger than those examined from cooler climates, including those from this study (Tables 3.15 and 3.16).

The reliability of growth curves are clearly dependent on the accuracy of the age determination techniques used to derive them, and consequently these curves may be less precise for bushbuck than for duiker. Nevertheless, growth patterns differ markedly between these two species, where for example asymptotic mass in male duiker is attained at 16 months (Table 3.13) approximately 50 months earlier than bushbuck (Table 3.10). Several factors are undoubtedly responsible for these differences, the most obvious of which relates simply to their relative sizes (Clutton-Brock and Harvey 1983). Another related factor concerns the different levels of social organisation displayed by these two species. Duiker exhibit territoriality (Chapter Eight) and many studies have shown that growth in territorial species virtually ceases at the time of sexual/social maturation (e.g. Robinette and Child 1964; Kerr 1965; Watson 1969; Hvidberg-Hansen 1970; Estes 1974; Penzhorn 1974). In contrast, all available data suggest that male dominance hierarchies, as evident in the bushbuck (Chapter Eight), are based on differential size achieved through prolonging growth

in adults (e.g. Pienaar 1969a; Estes 1974; Jarman 1974). This prolonged growth well beyond the onset of sexual maturity often results in sexual dimorphism, and is particularly pronounced in bushbuck and other Tragelaphus species.

Howells and Hanks (1975) have questioned the relevance of recording parameters that attain asymptotic values at an early age. These and subsequent authors (e.g. Hanks et al. 1976; Jeffery and Hanks 1981a; Attwell 1982a) have shown that hindfoot, ear and tail measurements are of dubious value in growth assessments, and the same conclusions can be drawn from this study. A knowledge of rates of growth in ear length is however, valuable when horn size is measured against ear length in the field. Asymptotic ear length is attained shortly after the initial appearance of horns in bushbuck, and is this a useful criterion, whereas asymptotic ear length in duiker is attained only when horns are over half their asymptotic length. Shoulder height and horn length are two other measurements that are of extremely limited use for the age determination of duiker in the field, but these two parameters are the primary means of subjective field classifications of female and male bushbuck respectively. In both species, body length and girth measurements may be useful for mass estimation purposes (Fig. 3.25) where weighing is impractical, while the direct measurement of mass is the most pertinent body parameter for growth and related studies. The value of body mass or carcass mass in condition assessments is discussed in Chapter Four, and the relationship between body mass and reproductive performance is considered in Chapter Five. Mass data have also demonstrated that maximum productivity occurs during the first year of life in duiker and female bushbuck, and during the first two years in male bushbuck, and in terms of meat production, the optimal age at which to harvest these animals would therefore be at one and two years respectively. However, these species are not as suitable as larger, more gregarious species for conventional game farming purposes, and their real commercial value is probably associated with sport hunting, when, in the case of bushbuck males at least,

they would be selected as much larger and older specimens.

The results of this study concur with the conclusions of Wilson et al. (1984) that it is virtually impossible to distinguish subadult from adult duiker in the field, since, with the exception of horn length and body mass, all other parameters have reached asymptotic values before 12 months of age. Although horn growth is more prolonged than any of the other parameters examined, horns are visible in 4-5 month old animals, and attain half their asymptotic length by 8 months of age.

Due to their prolonged growth and less individual variation in the younger age classes, bushbuck are considerably easier to classify in the field, although determining the ages of solitary females remains somewhat subjective. Problems of field age classification are further aggravated by the fact that both species breed throughout the year (Chapter Five). As a result of these limitations, and because the vast majority of animals were observed at night, it is highly probable that an unknown proportion of duiker and young bushbuck were incorrectly classified with respect to age and/or sex; the consequences of erroneous sightings are considered in Chapter Ten.

CHAPTER FOUR
CONDITION

4.1 INTRODUCTION

The physiological condition of an animal is closely related to its chances of living or dying (Hanks 1981) and is therefore an important factor influencing mortality (Klein and Olson 1960; Hirst 1969a; Klein 1970; Ferrar and Kerr 1971; Child 1972; Sinclair and Duncan 1972; Kruuk 1972; Franzmann and Arneson 1976; Hanks *et al*. 1976). In addition to mortality, the physiological condition of individuals within a population also has a direct effect on their rate of growth (e.g. Klein and Strandgaard 1972; Mitchell *et al*. 1976, 1977; Guinness *et al*. 1978a; Staines 1978; see Chapter Three), and reproductive performance (e.g. Verme 1965, 1969, 1977; Mitchell and Lincoln 1973; Mitchell and Brown 1974; Matschke and Roughton 1978; Mitchell and Crisp 1981; Ozoga and Verme 1982; Albon *et al*. 1983; see Chapter Five). All of these factors are inter-related (Hanks *et al*. 1976; Brooks 1978) and their interactive influences play an important role in determining the rate of population growth.

Using recognised methods of assessment, it is possible to compare the condition of two or more populations in different areas (Malpas 1977; Staines 1978; Weber *et al*. 1984), or to compare temporal changes in the same population (Klein 1968; Lowe 1971; Mitchell and Crisp 1981). Such comparisons may reflect the effects of past or current management, stocking rates or climatic influences (Smith 1970). Various parameters have been used or examined as potential indices of physiological condition, including deposited fat reserves, stored protein reserves, thymus gland size, adrenocortical hypertrophy, blood chemistry and haematology, and urinary excretion of hydroxyproline (Ozoga and Verme 1978; Hanks 1981). These are briefly reviewed below but are more comprehensively covered by Hanks (1981).

4.1.1 The Evaluation of Physiological Condition in Ungulates

4.1.1.1 Visual assessments related to external appearance

Several attempts have been made to classify the physiological conditions of live, unrestrained animals in the field (e.g. Riney 1960; Albl 1971; Keep 1971; Stanley Price 1974 cited in Coe 1983). However, as has been shown by Huntley (1971) and Hanks et al. (1976) such criteria are of limited value because stored fat reserves may be seriously depleted without being manifested in the external appearance of animals.

4.1.1.2 Deposited fat reserves

The measurement of deposited fat reserves has become an established method of condition assessment in ungulate species. Although the measurements of the total fat reserves of specific animals has been attempted (Smith and Ledger 1964; Smith 1970; Finger et al. 1981), such a procedure is extremely tedious, expensive and time consuming, and the quantification of more localised fat reserves has been more frequently practiced. These include subcutaneous, visceral, perinephric and bone marrow fat deposits. Measurements of subcutaneous and visceral fat deposits have largely been confined to temperate species (e.g. Anderson et al. 1972a; Dauphine 1976; Mitchell et al. 1976; Hewson and Verkaik 1981; Stribling et al. 1984; see Plate 2a) but such deposits are usually less pronounced in African game species, which tend to have a much lower overall fat content (Huntley 1971; see Plate 2b). Riney's (1955) kidney fat index (mass of perinephric fat expressed as a percentage of kidney mass) has been widely used and evaluated in a number of ungulate species (e.g. Ransom 1965; Caughley 1970a, 1971; Flook 1970; Albl 1971; Bear 1971; Blood and Lovaas 1971; Huntley 1971; Anderson et al. 1972a; ; Sinclair and Duncan 1972; Dauphine 1975; Laws et al. 1975; Williamson 1975; Hanks et al. 1976; Mitchell et al. 1976; Brooks et al. 1977; Brooks 1978; Attwell 1982a; Barrett 1982; Dunham and Murray 1982). Smith

PLATE 2 (a) Subcutaneous fat reserves of a 2,5 month old reindeer from Svalbard, autumn 1983. (Photograph taken by N.Tyler)

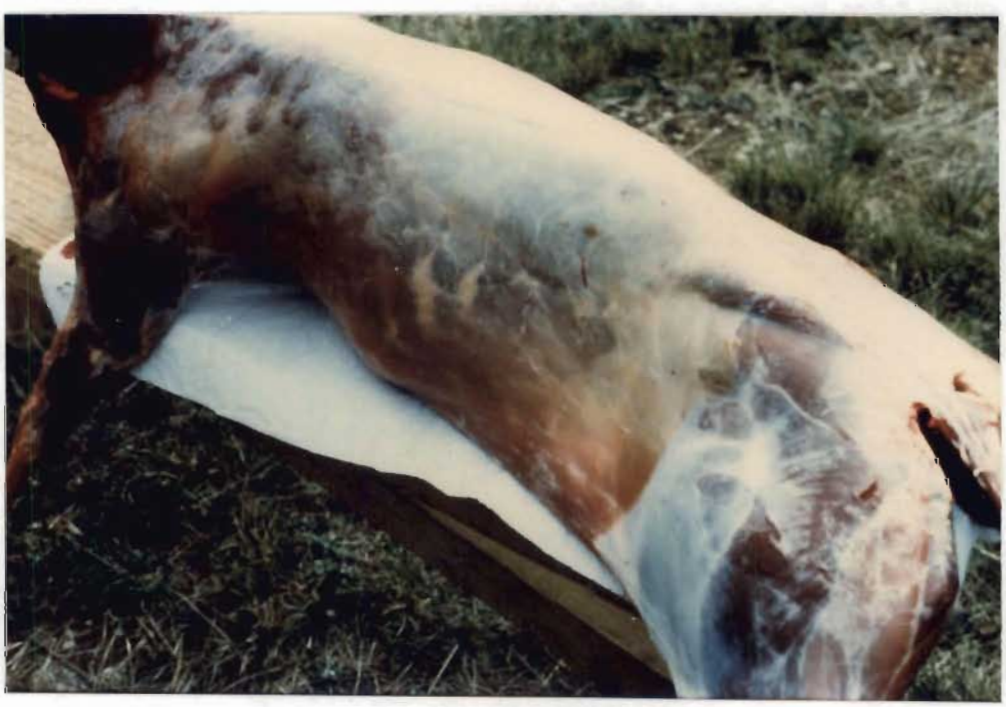


PLATE 2 (b) Subcutaneous fat reserves of a 48 month old female bushbuck from Weza, autumn 1984. (Photograph taken by J.Hanks)

(1970) examined stored fat reserves in ten ungulate species and found significant correlations between kidney fat and total body fat in eight of these, concluding that the kidney fat index best fulfilled the needs of a workable technique. Finger et al. (1981) also found a significant correlation between perinephric fat and total body fat reserves in white-tailed deer and several other authors considered perinephric fat to be the most satisfactory means of rating body condition (Caughley 1970a; Monson et al. 1974).

Kidney fat indices have several limitations however. In addition to reflecting seasonal variations in nutritional status, perinephric fat reserves can be influenced by physiological and behavioural events associated with reproduction (Caughley 1970a; Bear 1971; Hanks et al. 1976; Hanks 1981), and Anderson et al. (1972a) concluded that the extreme variability of mule deer kidney fat indices limited their usefulness as indices to detect annual or seasonal changes in mean carcass fat. Other studies of cervids have shown that kidneys may undergo such pronounced seasonal fluctuation in mass (possibly in response to changing photoperiod, see Abbott et al. 1984) that they are unsuitable as a measure of body size, and unless allowance is made for these changes, seasonal comparisons of kidney fat indices are rendered invalid (Batcheler and Clarke 1970; Dauphine 1975, 1976; Meadows and Hakonson 1982). Although not unique to perinephric fat reserves, several authors have shown that young, growing animals have significantly lower kidney fat indices than adults collected at the same time, and consequently suggested that inter-seasonal comparisons should be confined to the adult segment of the population (Hanks et al. 1976; Brooks 1978; Attwell 1982a; Dunham and Murray 1982; Johns et al. 1984). Finally the reliability or predictability of the kidney fat index decreases as perinephric fat reserves decline (Ransom 1965; Sinclair and Duncan 1972; Mitchell et al. 1977; Mitchell and Crisp 1981). Since bone marrow fat is mobilized after kidney fat (Harris 1945; Bear 1971), the former provides a better measure for animals in intermediate or poor condition (Brooks et al. 1977; Hanks 1981).

The fat content of bone marrow was initially assessed qualitatively by colour and texture (Cheatum 1949; Riney 1955) and although the same method has been used in more recent times (Huntley 1971; Els 1973; Mitchell et al. 1976) this technique is commonly considered to be reliable only for extreme fat values (Bear 1971; Verme and Holland 1973; Franzmann and Arneson 1976). Semi-quantitative methods of marrow fat assessment have been proposed (Greer 1968; Leuth 1973 cited in Stribling et al. 1984), but until Neiland's important contribution in 1970, the only quantitative means of fat measurement involved conventional fat extraction procedures, which are fairly time consuming and costly. Neiland (1970) demonstrated that marrow is a three-component system comprising fat, water and non-fat residue, and that the dry mass of the marrow, corrected for non-fat residue, provides an adequate measure of marrow fat content. This technique has been subsequently used by Sinclair and Duncan (1972), Hanks et al. (1976) and Brooks et al. (1977), who used the general formula:

$$\% \text{ marrow fat} = \% \text{ dry mass} - 7$$

to estimate bone marrow fat in eight African ungulates. Their formula has been adopted in a number of other ungulate studies (e.g. Reich 1981; Howard 1983), and both Sinclair and Duncan (1972) and Brooks et al. (1977) suggested that such a prediction may be generally applicable to other tropical ruminants.

Verme and Holland (1973) independently developed another method, reagent-dry assay, for quantifying the fat content in bone marrow and found, together with Hunt (1979) that results from this technique were comparable to those obtained from both ether extraction and dry-mass analyses.

As with kidney fat indices, bone marrow fat is of limited use as a measure of condition in younger animals (Dauphine 1976; Franzmann and Arneson 1976; Hanks et al. 1976; Fong 1981; Dunham and Murray 1982). However, in

addition to being a more sensitive measure for animals in poor condition, marrow samples are of obvious value in predation studies (Reich 1981) and in condition analyses of carcasses from animals that are found several days after death (Kie 1978).

Harris (1945) and Riney (1955) have described a sequential pattern of fat mobilization in ungulates, commencing in the subcutaneous regions and progressing to the abdominal, perinephric and finally bone marrow reserves. This sequence has been confirmed and described in more detail by Ransom (1965), Sinclair and Duncan (1972) and Brooks et al. (1977). Brooks et al. (1977) also demonstrated that sequential mobilization may occur within the long limb bones, with proximal bones showing distinct fat loss before medial and distal marrow fat is utilized. These findings were confirmed by Reich (1981) who also found that marrow fat reserves in the hind limb were utilized at a faster rate than comparable bones in the fore limb. As a result, careful consideration should be given to the selection of bone marrow samples for comparative purposes (Brooks et al. 1977).

4.1.1.3 Total mass and stored protein reserves

Measures of body mass were one of the first parameters to be used in physiological condition estimates (Park and Day 1942 cited in Hanks 1981; Severinghaus 1955) and remain, albeit in an often modified form, one of the more universally used criteria for reflecting growth rates and nutritive status of cervids today (Klein 1970; Lowe 1971; Reimers 1972; Roseberry and Klimstra 1975; Wegge 1975; Mitchell et al. 1976; Staines 1978; Mitchell and Crisp 1981; Kie et al. 1983; Weber et al. 1984). Klein (1968) provided one of the best examples of the value of body mass measurements as an index of condition, and quoted numerous examples of large body size being correlated with high quality of forage (Klein 1970). Kie et al. (1983) concluded that, from an extremely comprehensive list of parameters, body mass measurements, Kidney fat and marrow fat were the best indicators of

physiological condition using post mortem sampling.

Where total mass measurements are impractical, the mass of dimensions of selected muscles have successfully been used to determine stored protein reserves (Hewson and Verkaik 1981; Sharp 1982).

4.1.1.4 Adrenocortical hypertrophy

During the last two decades, studies of ungulates have been cautious or inconclusive in their interpretation of adrenal mass changes in relation to physiological condition (Welch 1962; Flook 1970; Smith 1970; Anderson et al. 1971; Klein and Strandgaard 1972; Verme and Ozoga 1980b; Hanks 1981; Kie et al. 1983; Seal et al. 1983), although with small mammals it is generally accepted that adrenal hypertrophy and hyperplasia are reactions of the body to stress, and that an increase in adrenocortical tissue has a direct relationship to adrenal mass (Christian 1955). However, a variety of other factors unrelated to the quality and quantity of social interactions will influence adrenal mass, including low temperature, sexual activity, photoperiod and diet (Hanks 1981; Plotka et al. 1983; Abbott et al. 1984).

4.1.1.5 Analyses of blood and urine

The use of blood analyses as indicators of physiological condition has gained in popularity during recent years, not only in ungulates (e.g. Anderson et al. 1972b; Seal et al. 1972; McCullagh 1973; Coblentz 1975; Cooper et al. 1975; Pedersen and Pedersen 1975; deCalesta et al. 1977; Wilson and Hirst 1977; Franzmann and LeResche 1978; Warren et al. 1981; Melton and Melton 1982a; Kie et al. 1983) but also in primates (Melton and Melton 1982b) and carnivore studies (Seal et al. 1975; Seal and Mech 1983).

One of the main reasons for this increased attention is undoubtedly associated with the fact that fat and stored

protein reserves do not necessarily reflect the environmental resources at the time of sampling (Malpas 1977), and that such reserves may in any case be of limited diagnostic value at all times of the year (Ozoga and Verme 1978). However, several of the authors cited above obtained inconclusive results from blood analyses (e.g. Warren et al. 1981; Kie et al. 1983; Seal et al.1983; Seal and Mech 1983) and unless the blood is collected from animals with known nutritional histories, it is usually impossible to relate blood parameters to environmental variables, physiological condition, or demographic vigour (Hanks 1981; Warren et al. 1981).

The amino acid hydroxyproline is derived from the breakdown of collagen, and its detection in urine analyses has been used to provide an index of growth and nutrition in elephants (McCullagh 1969; Malpas 1977).

4.1.2 Estimates of Mortality

It is extremely useful for the wildlife manager to know the maximum life-span of an animal and how life expectancy varies by sex and age under different environmental conditions. Such information is usually summarised in the form of life tables (Caughley 1966, 1976, 1977; Eberhardt 1969), which may be either dynamic or time-specific (nomenclature follows Eberhardt 1969;Lowe 1969). In dynamic life table analysis, it is necessary to record the age at death of every individual in a cohort from birth to the death of the last survivor. This is rarely practical in most studies of large mammals due to their longevity (Hanks 1979; Sinclair and Grimsdell 1982; Spinage 1982). The time-specific life table considers the mortality of each age class in a given population over a certain time interval, and usually represents no more than a crude generalisation of the structure of that population at the time when the data were collected: it provides no indication of how that structure was attained, or what its future pattern might be (Spinage 1972b, 1982). Furthermore, time-specific life tables are

only representative when the population is stationary in size (Sinclair and Grimsdell 1982). Consequently the inferences that can be drawn from time-specific life tables may be somewhat limited. Nevertheless, time-specific life tables are frequently constructed in wildlife studies, and may be based on material obtained either from a culled sample of a living population (e.g. Caughley 1970b, 1971; Anderson 1978; Dapson et al. 1979; Attwell 1982b; Simmons et al. 1984) or from a collection of found skulls (e.g. Lowe 1969; Spinage 1970, 1972b; Sinclair 1977; Skogland 1985). Both methods of data collection are subject to sampling bias. In skull collections, infants are invariably under-represented because their skulls deteriorate (or are consumed by predators and scavengers) at a faster rate than those of adults (Caughley 1966, 1976; Bradley and Baker 1967 cited in Leslie and Douglas 1979; Spinage 1968; Verme 1977; Hanks 1979; Melton and Melton 1982a). Similarly, female skulls may be less robust than those of males (Spinage 1970). Shot samples may be biased by behavioural differences between the sexes and between different age classes (e.g. lying out behaviour of infants), age differences (younger animals by virtue of their size are usually less conspicuous and therefore may not be detected) and because of the humane aspects of collecting sucklings (Leader-Williams 1980). Finally, it should be noted that not all authors have accepted the term dynamic life table. Spinage (1982) refers to this procedure as an age-specific life table but unfortunately this term has not been used consistently: Sinclair and Grimsdell (1982) interchange the meanings of time- and age-specific life tables as given by Spinage (1982) while Eltringham (1979) refers to time- and age-specific life tables when the data are obtained from skull collections and culled material respectively.

Numerous other authors have used these same techniques of data collection even where unknown population growth rates preclude life table calculations, or where the emphasis is rather on causes of mortality (e.g. Klein and Olson 1964; Martinka 1967; Flook 1970; Miller and Broughton 1974; de Bie 1976; Mitchell and Staines 1976; Crowe and Liversidge 1977;

Wolfe 1977; Woolf and Harder 1979; Mitchell and Crisp 1981; Barrett 1982; Clutton-Brock and Albon 1982; Bartmann 1984). Mortality rates can also be estimated by monitoring the fates of marked individuals, provided that it can be shown that capture and marking methods have little effect on subsequent survival (Downing and McGinnes 1969; White et al. 1972; Beale and Smith 1973; Goldberg and Haas 1978; Hamlin et al. 1982). While some studies have used visual markers (e.g. LeResche 1968; Kimball and Wolfe 1974; Kie et al. 1979; Woodson et al. 1980; Bailey and Franzmann 1983; Sauer and Boyce 1983; White and Bartmann 1983), other authors have found that radio telemetry may greatly facilitate the collection of such data, either through regularly locating the subjects (e.g. Mech 1967; Cook et al. 1971; Beale and Smith 1973; Trent and Rongstad 1974; Brand et al. 1975; Carroll and Brown 1977; Hoskinson and Tester 1980; Steigers and Flinders 1980; Ballard et al. 1981; Hauge and Keith 1981; Ozoga et al. 1982a; Cederlund and Lindstrom 1983; White 1983; Barrett 1984) or by motion- or temperature-sensitive telemetry (Knowlton et al. 1968; Kolz 1975 cited in Mech 1968; Stoddart 1970; Tzilkowski and Knowlton 1979; Franzmann et al. 1980).

4.1.3 Previous Studies of Bushbuck and Duiker Condition and Mortality

Remarkably little attention has been centered on the physiological condition or rates and causes of mortality in these two species. Allsopp (1970) concluded from a shot sample of 46 females that the population under study was "decreasing at a rate of about 2% per year", and ascribed this to control measures and private hunting. Other bushbuck studies involving mortality have largely concentrated on identifying the main predators of this species (Wilson and Child 1964, also see Mitchell et al. 1965; Pienaar 1969b) or at best the effects of predation on bushbuck populations, which was estimated by Simpson (1974c) to be less than 10% per annum.

Morris (1973) assessed the condition of an unspecified

number of bushbuck using kidney fat indices and adrenal gland mass. These perinephric fat measurements were all collected during one month, and although females over the age of 12 months had significantly higher KFI's than males of comparable age, Morris (1973) noted that these were very variable in both sexes. Morris (1973) also found no significant relationship between KFI and adrenal mass, but reported that relative adrenal mass values were highest in immature bushbuck, and higher in adult females than in mature males. Odendaal (1977) examined the concentrations of six essential elements in bushbuck liver samples, and provided a list of the arthropod parasites occurring on this species in the southern Cape.

Relevant data for duiker are even more scarce. Wilson (1966b) listed 18 predators of this species, but only considered two (leopard and wild dog) as important. Other examples of predation on the duiker have been given by Mitchell et al. (1965) and Pienaar (1969b). In the only published account of physiological condition in this species, Schmidt (1984b) concluded that "common duiker in Natal retain good physiological condition throughout winter". His findings were however, based on only six adult and seven subadult animals, all of which were presumably collected during the "late winter study".

4.2 METHODS

4.2.1 Condition

4.2.1.1 Deposited fat reserves

Perinephric fat measurements were recorded from 132 bushbuck (68 males and 64 females) and 116 duiker (60 males and 56 females), that were randomly culled within the confines of Weza State Forest. Additional data were available from 25 bushbuck (12 males, 13 females) and 4 duiker (3 males, 1 female) that died of unnatural (i.e. accidental) causes within both intensive and extensive study

areas. Fat reserves from 47 male bushbuck and 19 duiker (11 males, 8 females) that were shot on adjacent farms during the hunting season (31st May to 31st August) were treated in an identical manner but this material was analysed separately for comparative purposes (see below).

After removing the intestines, each kidney was pulled out of the body cavity using the "grab method", i.e. without trimming but allowing the anterior and posterior extension of the fat to come away naturally (Hanks et al. 1976). Capsular fat and a small amount of connective tissue was then separated from each kidney , and was used to calculate the kidney fat index (KFI), where

$$KFI = \frac{\text{total mass of perinephric fat}}{\text{mass of both kidneys}} \times 100$$

Kidneys and perinephric fat were weighed to the nearest 0,01g on a triple beam balance. All kidneys that were damaged were discarded, and thus the KFI values for those individuals were not calculated.

Since the carcasses of both bushbuck and duiker shot at Weza were sold as venison by the Department of Forestry, the collection of bone marrow samples was confined to the forelimbs. Whenever possible, samples were collected from all three long bones of the right forelimb, but if these had been extensively damaged, samples were instead taken from the intact bones of the left forelimb. Bone marrow samples were collected from a total of 132 bushbuck (69 males and 63 females) and 101 duiker (56 males and 45 females). Each series of bones was labelled with metal tags and frozen until they could be processed, at which time they were sawn open and the middle third section of marrow removed. Care was taken to avoid haemopoietic tissue or bone fragments and dust. Each sample was allowed to defrost in a preweighed bottle, and was then weighed to the nearest 0,01g. Fresh marrow samples varied in mass according to species, site of

collection and age of individual, but ranged from 0,10g to 10,29g and 0,09g to 2,32g in bushbuck and duiker respectively. These samples were then dried in an oven at 100°C for at least 10 days until a constant mass was achieved. The dried mass of each sample was expressed as a percentage of the fresh mass. A selected sub-sample of dried marrows (which included specimens with a broad range of percentage dry mass values, see below) were transferred to a Soxhlet apparatus where fat was extracted with Petroleum Spirit (b.p. 40°C - 60°C) for at least eight hours. The residue from each sample was then dried and weighed, and the fat content was derived from the difference in mass before and after extraction. This was also expressed as a percentage of the fresh mass. The poor relationship between percentage dry mass and percentage fat content from some of the bones examined at Weza prompted additional analyses to be conducted elsewhere, and slightly less than 50% of the 55 bushbuck and 45 duiker marrow samples were analysed in an identical manner in laboratories at the University of Natal and Cedara Agricultural College. These independent analyses did not improve the relationship between percentage dry mass and percentage fat content, and all data were subsequently pooled according to source (i.e. humerus, radius or metacarpus).

Several studies have demonstrated that fat reserves in young, growing animals may be significantly lower than those from adults collected at the same time (e.g. Flook 1970; Franzmann and Arneson 1976; Hanks et al. 1976; Dunham and Murray 1982). Consequently, at the start of this study, the collection of marrow samples was confined to animals with permanent dentition. This practice resulted in a high proportion of duiker samples being discarded (see Chapter Ten) and was subsequently altered to include all duiker that had attained at least 95% of their asymptotic mass. These included all males and females over the age of 17,5 months (Chapter Three). Relatively high KFI's were recorded from several younger duiker during the course of this study, and since in several instances these were comparable to adult duiker values, it was decided to examine the influence of age

on deposited fat reserves further. Consequently, bone marrow samples were analysed from 17 subadult (under 30 months old) bushbuck (eight males and nine females) and 20 duiker younger than 20 months old (eight males and 12 females). These younger animals have been included in the overall sample sizes detailed above.

Kidney fat data were also recorded from 47 male bushbuck and 19 duiker (eleven males and eight females) that were shot on neighbouring farms during the hunting seasons (June to August) of 1981 to 1983. Forty of the male bushbuck and 13 of the duiker were older than 30 months and 17,5 months respectively. Marrow samples were taken from the metacarpus of 36 adult male bushbuck and from all of the adult duiker. These data were collected to compare indices of physiological condition from populations under differing levels of management. Although several of the farms had similar habitats to Weza, including extensive pine plantations and indigenous forests, they included much higher proportions of wattle and gum stands, and also contained varying areas of arable crops and grazing. Several of the farms also planted supplementary feed specifically for wildlife consumption, and these together with provisions for livestock and cash crops, were extensively utilized (Chapter Six). Hunting of bushbuck was confined to males (approximately 40 rams were harvested per annum) and was orientated towards older (i.e. obviously adult) animals. In contrast, both male and female duiker of all ages (with the exception of infants) were hunted on these farms and approximately 30 animals were harvested per annum.

4.2.1.2 Stored protein reserves

Since the relationship between total body mass and "carcass" mass was found to be highly significant for both bushbuck and duiker (see Chapter Three), the additional effort required to reweigh each carcass was deemed unnecessary, and the former measurement was therefore used for condition assessment purposes. Because of the variable influences of growth, pregnancy and lactation, total body

mass data from subadult males and all females of both species were not analysed. All adult male measurements were taken following the procedure detailed in section 3.2.6.

Additional adult male mass measurements were also recorded from 32 bushbuck and 5 duiker shot on adjacent farms during the winter months of 1982 and 1983.

The fresh mass of a specific muscle, the flexor carpi ulnaris, was also examined as a potential means of assessing stored protein reserves. This muscle was severed at the tendons of origin and insertion, cleaned of all superficial connective tissue, and weighed on a triple beam balance to 0,01g . The length of the radius was also recorded (to the nearest 1 mm) and a muscle index (MI) was calculated as:

$$MI = \frac{\text{fresh mass of muscle(g)}}{\text{length of radius}} \times 100$$

Muscle indices were calculated from 14 bushbuck and 11 duiker. No meaningful relationship was found between MI and total body mass or MI and any of the fat reserve measurements. Attempts to isolate a more suitable muscle were hampered by the fact that whole carcasses were sold as venison. (However, a more faculative muscle would probably exhibit greater fluctuations in mass, and would therefore be more suitable as an index of condition (Berg and Butterfield 1976 cited in Sharp 1982)). As a result of these limitations, the use of the MI was abandoned in this study.

4.2.1.3 Adrenocortical hypertrophy

Adrenal glands were collected from 144 bushbuck and 106 duiker. These were dissected out and each intact gland was weighed to the nearest 0,01g. A small incision was made through the cortex and medulla to facilitate fixation in buffered neutral formalin for subsequent histological examination. The specimens were dehydrated in alcohol,

cleared in xylene, embedded in "Histosoc" medium, sectioned at 7µm, and stained with Mayer's haematoxylin and 1% alcoholic eosin. Prepared microscope slides of the stained sections of adrenals were placed in an Axomat 4 photographic enlarger, the magnification was fixed by maintaining a constant focal distance of the enlarger, and the image was traced onto paper.

The relative area of the cortex and medulla in each adrenal gland section was measured initially by a 9864 A digitizer attached to a Hewlett Packard 9830 A which was programmed to measure areas of tissue in mm^2. These data were subsequently converted into a cortex/medulla ratio for each specimen. Subsequently, using identical conversion factors, a Planix 7 planimeter was used for area determinations. An adrenal index was calculated as mass (mg) of the adrenal gland per 100g of body mass.

4.2.1.4 Blood analyses

A number of difficulties associated with the collection and analyses of blood were encountered during this study. These included problems in the night time collection of uncontaminated blood from animals shot in the neck with a high velocity sporting rifle, lapses in the availability of suitable laboratory equipment needed for such analyses, local power failures resulting in the rejection of thawed serum samples, and the high financial costs incurred in performing blood chemistry tests. As a result of these restrictions, and because several blood chemistry parameters are of little or dubious value to assessments of physiological conditions (see above), blood collections were discontinued after samples had been obtained from 27 bushbuck and 36 duiker. Packed cell volume (P.C.V.) values were obtained from all of these animals in the standard medical manner (i.e. by centrifugation). However, since P.C.V. values are most useful in the diagnosis of various pathological conditions (Hanks 1981), these findings (together with limited parasitology data) were submitted to Dr. M. Keep, Natal

Parks Board, who conducted a detailed parasitological survey of the bushbuck and duiker at Weza during 1983 and 1984, and are thus not considered here.

4.2.1.5 Live animals

Although Riney (1960) found that duiker could be separated into three classes of condition (good, fair and poor), similar distinctions could not be made for either duiker or bushbuck at Weza, when both species were most commonly observed at night. Riney's (1960) method was however employed in assessments of the condition of immobilized animals. In order to minimize recumbency time no attempt was made to collect blood from immobilized animals, which in any case may show aberrant blood values as a result of immobilization and stress (Franzmann and Thorne 1970; Seal et al. 1972; Melton and Melton 1982a).

4.2.2 Mortality

Initially, because of the areas involved, the diversity of the habitats and the dense nature of the vegetation, systematic searches for carcasses were not considered practical, and dead bushbuck and duiker were simply found during routine aspects of field work. Later, once known patterns of movement had been established, intensive localised searches were conducted on foot or horseback for those collared animals that had suddenly disappeared. Similarly, radio collared animals were searched for if their location (determined by triangulation) did not alter over a period of several days. Searches for radio collared animals were greatly facilitated by the use of a hand-held collapsible, dipole antenna, and were continued until either the carcass or collar of the animal had been found, or until the live animal had been seen. Details of the telemetry equipment and radio tracking techniques that were employed are detailed in Appendix D.

The author was also notified of animals that were killed in road accidents, found in snares, or killed by dogs. Forestry staff also assisted in the recovery of several collars, although these were often returned without the skull. Several forest guards and labourers provided the localities of fresh carcasses, and some of the foresters kindly collected the skulls of all bushbuck and duiker found in the field, irrespective of whether the animal had been collared or not. Attempts to standardise and maximise the collections of skulls from the field were largely unsuccessful. Proposals offering a financial reward for each skull that was brought in were rejected by local management staff on the grounds that such incentives would encourage poaching. Consequently, with the exception of data from radio collared animals, no quantitative estimates of mortality could be determined from carcasses collected during this study.

It was usually possible to determine the cause of death only if reasonably fresh carcasses were found. It was also generally easier to identify mortalities caused by unnatural rather than natural factors (e.g. road accidents, poaching). Bushbuck and duiker were considered to have died from starvation if they had severely depleted fat reserves and had died during the winter or early spring. Animals dying from exposure were found in a state of inanition during or immediately following extreme winter conditions (that were often associated with high levels of precipitation). Predation was considered to be the cause of death only when wounds were visible on a carcass. Animals killed by lynx were recognised by scratch and bite marks around the head and neck, and where flesh had been eaten from the rear of the animal (Grobler 1981) . Animals killed by dogs (no lacerations on the body, and meat taken from the forelimbs and chest) were considered to have been poached and therefore recorded as unnatural deaths.

Following the procedures detailed above, and whenever possible, fat and protein reserves, and adrenal glands were measured from each carcass that was found in the field.

4.3 RESULTS

4.3.1 Kidney Mass in Relation to KFI

Before proceeding with the use of the KFI, the extent to which kidney mass might vary during the year (and hence potentially distort the reliability of this means of assessment) was examined. There were no significant seasonal differences in the kidney mass of adult male and female duiker and adult female bushbuck, but kidneys from adult male bushbuck were significantly heavier in summer than in spring ($t=2,364$; $p<0,05$). However, perinephric fat deposits of male bushbuck were most extensive during the summer months and most depleted during spring (see below), and consequently this variability was considered to have a negligible effect on subsequent results, particularly when identical seasonal trends were evident from independent methods of condition assessment.

4.3.2 Mass in Relation to Fat Content of Bone Marrow

In bushbuck the relationship between the percentage dry mass and the percentage fat content of the humerus marrow had a high positive correlation ($r=0,989$; $p<0,001$) but gave a much lower, but still significant, correlation for the radius ($r=0,762$; $p<0,01$) and metacarpus ($r=0,552$; $p<0,01$). These relationships are illustrated in Fig. 4.1. A similar trend was evident in the marrow samples from duiker (Fig. 4.2) except that there was no obvious relationship between percentage dry mass and percentage fat content of marrow from the metacarpus. Consequently, while the dry mass of humerus marrow was a good quantitative estimate of its fat content, accurate predictions of fat content could not be determined from the percentage dry mass of radius or metacarpus marrow from either species. Unfortunately, financial and manpower constraints precluded the determination of fat content by Soxhlet extraction for each individual bushbuck and duiker, and instead, for comparative purposes, all marrow samples collected in this study have been expressed as percentage dry

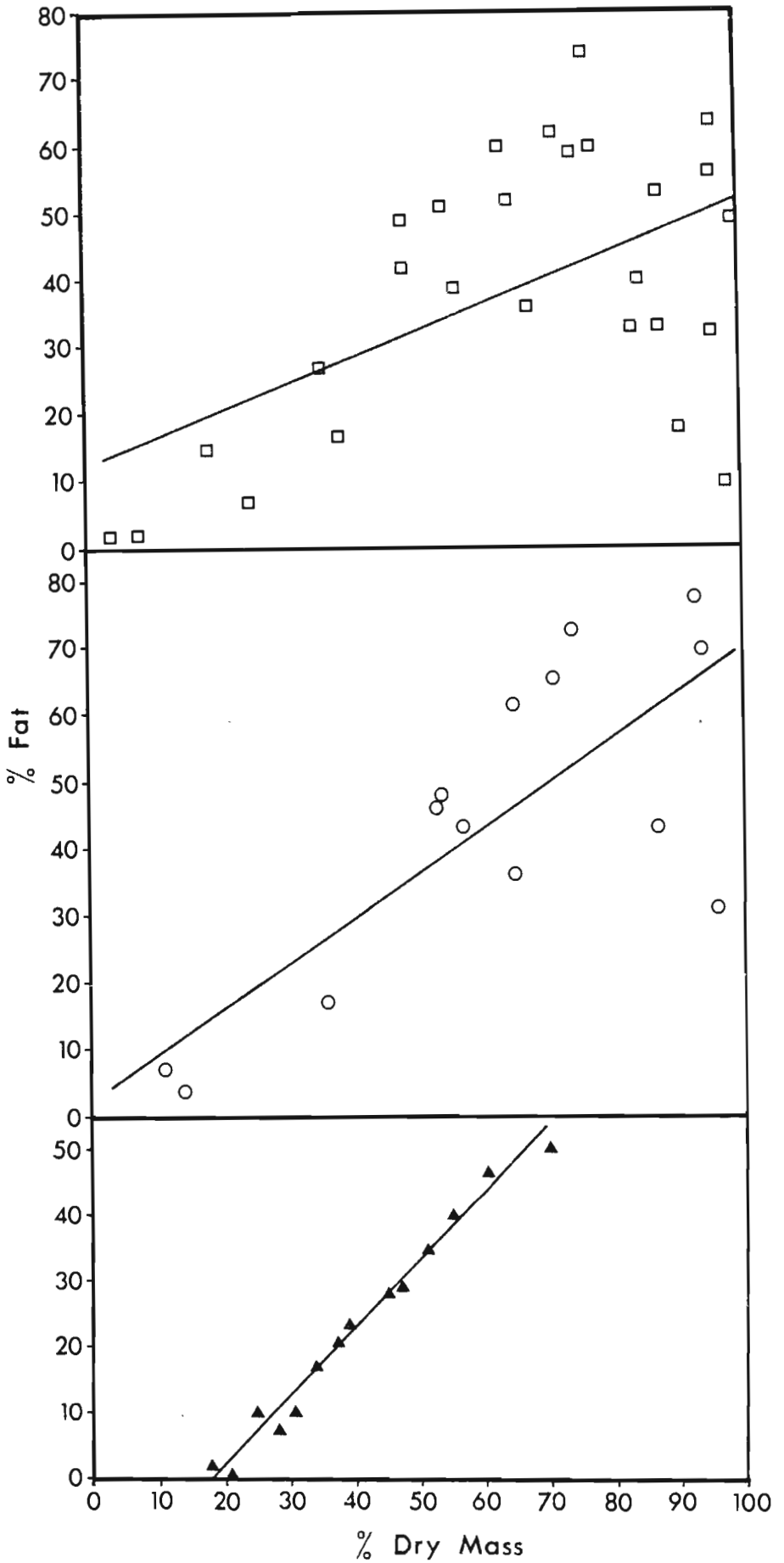


FIGURE 4.1 The relationship between % fat content and % dry mass in bushbuck bone marrow (closed triangles - humerus; open circles - radius ; open squares - metacarpus).

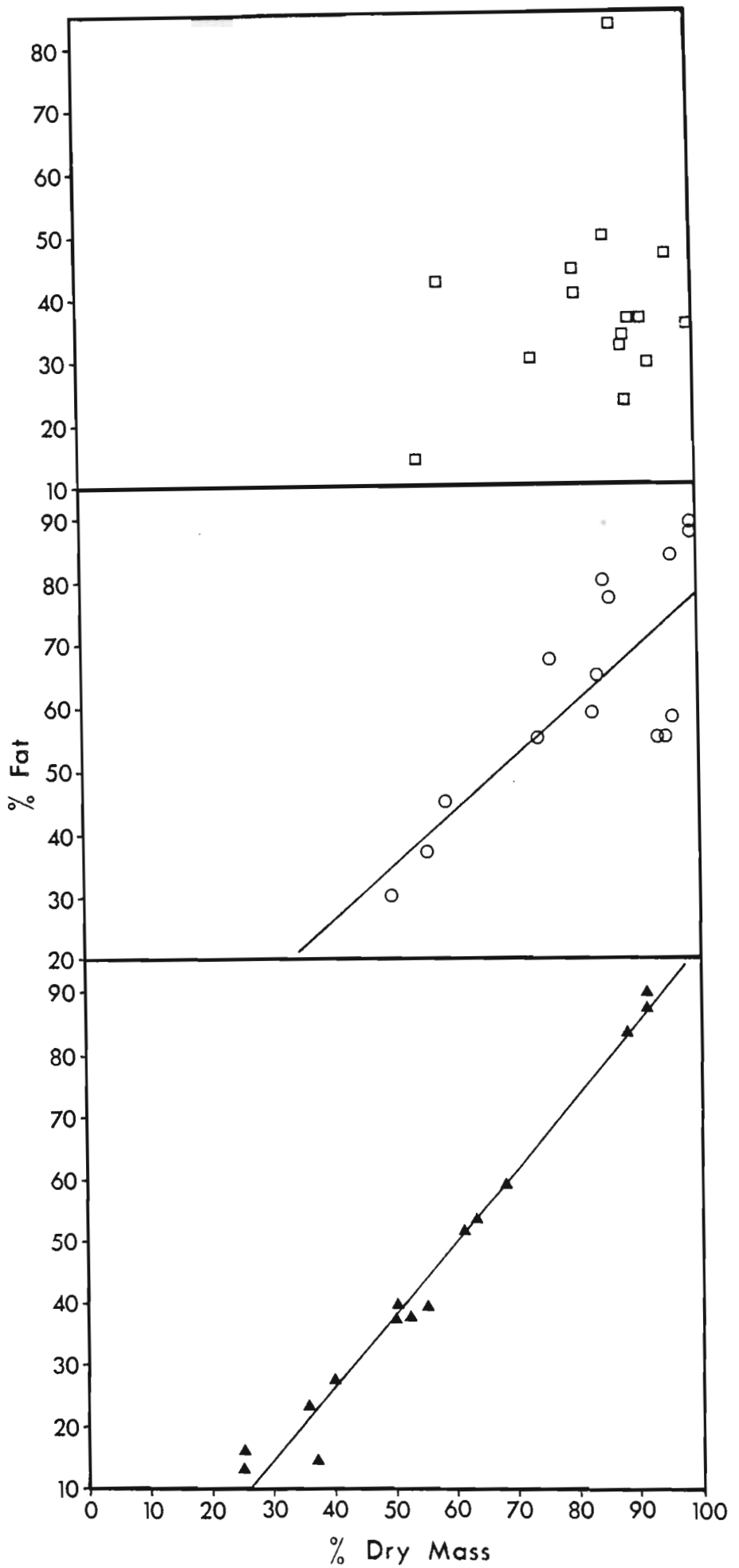


FIGURE 4.2 The relationship between % fat content and % dry mass in duiker bone marrow (closed triangles - humerus; open circles - radius ; open squares - metacarpus).

mass (% DM), with due cognizance of the fact that these values may not provide an absolute estimate of deposited fat reserves.

4.3.3 Sequential Mobilization of Fat Reserves

A high proportion of bushbuck had low KFI, intermediate % DM values from the humerus, and high % DM values from the radius and metacarpus (Fig. 4.3). This suggests that bone marrow fat is utilized sequentially, with the proximal bone showing depleted fat reserves before fat is mobilized from the medial and distal bones. In order to examine this phenomenon further, KFI's were plotted against % DM values from the humerus, radius and metacarpus. There was no obvious relationship between KFI and % DM of the humerus in either adult male or adult female bushbuck, and although animals with KFI's greater than 30 had % DM values in excess of 25%, bushbuck with KFI's lower than 20 had % DM values varying from 12% to 79% (Fig. 4.4). The % DM values from the radius and metacarpus however, remained high (80%+) while the KFI declined to a value of approximately 20, but below this value, the % DM from both bones showed considerable variation (Figs. 4.5 and 4.6). These findings demonstrate that perinephric fat is indeed utilized before marrow fat, and that the latter therefore provides a better means of assessing condition once KFI's have declined below a value of 20.

The relationship between % DM of the humerus and % DM of the radius is shown in Fig. 4.7. None of the bushbuck examined had a % DM from the humerus in excess of 80%, while only six animals had values below 20%, indicating that all available fat had been utilized from this bone (see 4.3.2). Fat was generally mobilized from the radius once the % DM of the humerus fell below 50%.

There was a very good and highly significant relationship between % DM of the radius and % DM of the metacarpus for both male and female bushbuck. These are

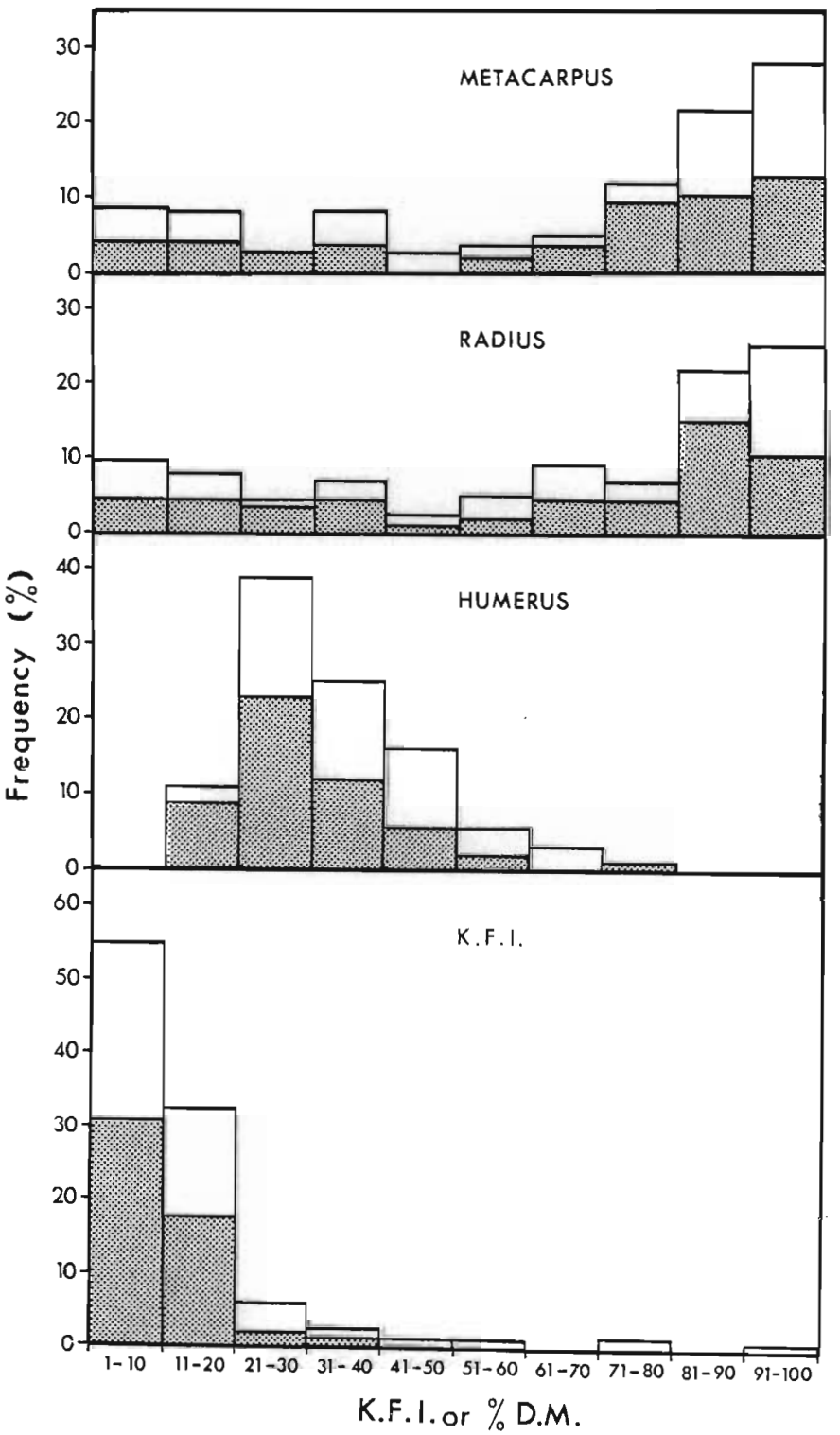


FIGURE 4.3 Frequency distribution of KFI and % DM values of bone marrow from bushbuck culled at Weza (shaded portion represents males).

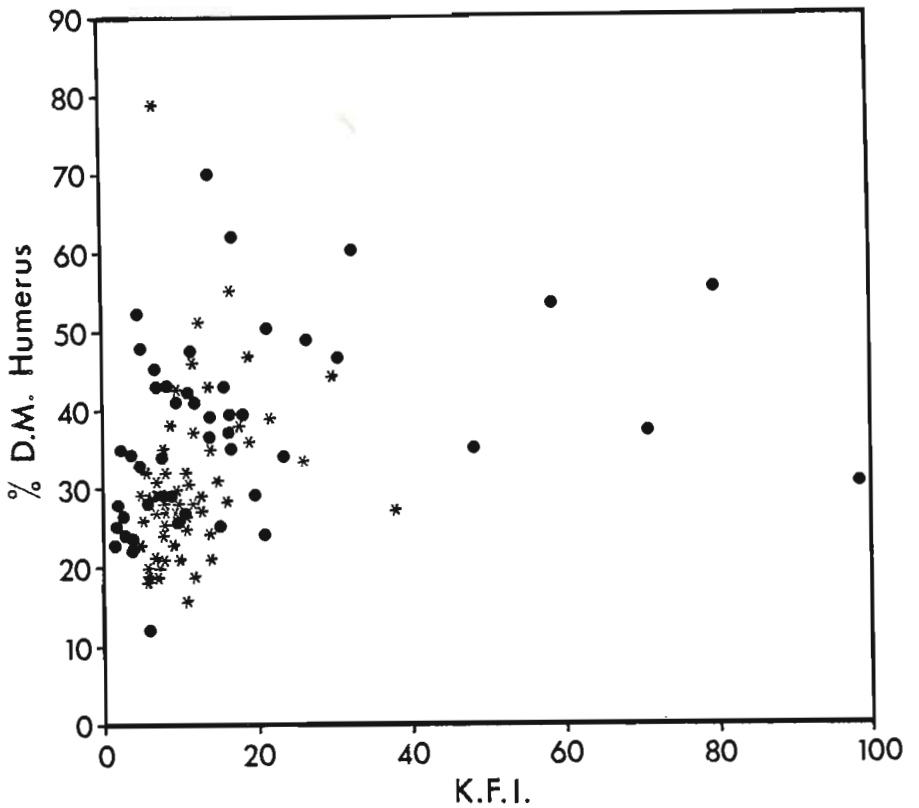


FIGURE 4.4 The relationship between KFI and % DM of marrow from the humerus of male (asterisk) and female (closed circle) bushbuck.

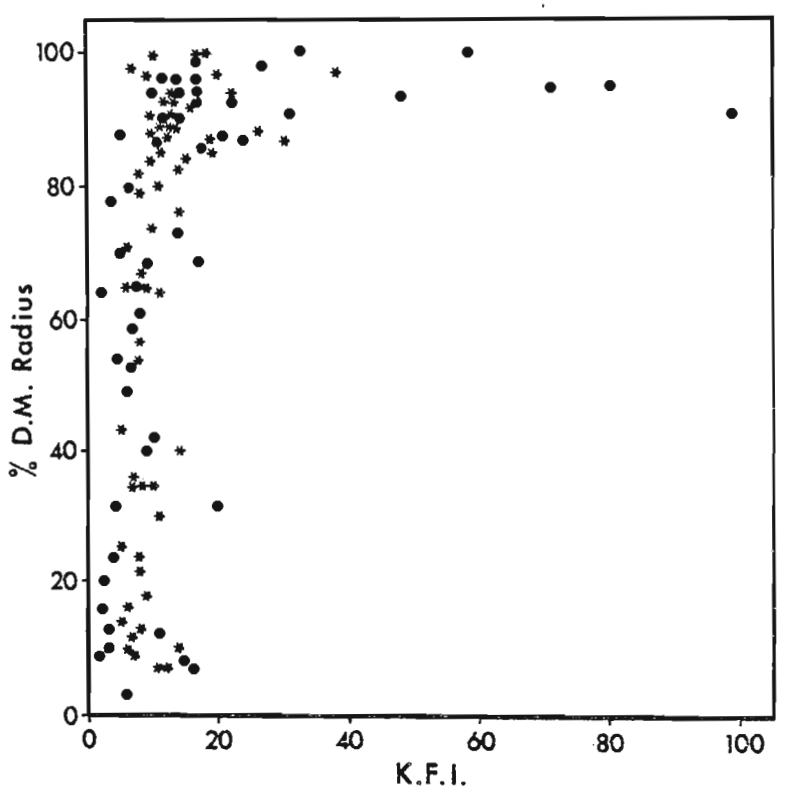


FIGURE 4.5 The relationship between KFI and % DM of marrow from the radius of male (asterisk) and female (closed circle) bushbuck.

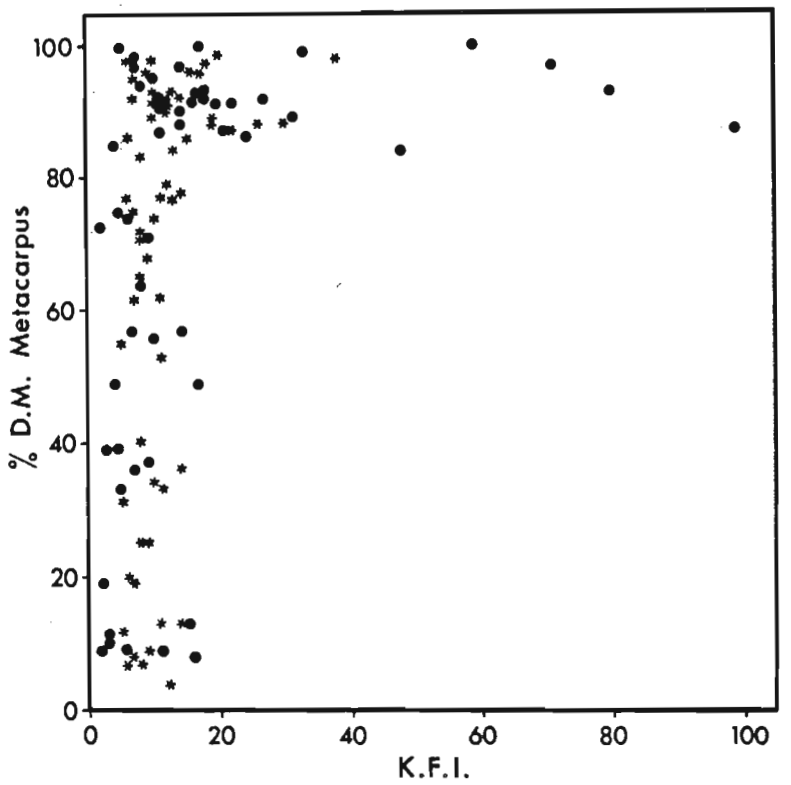


FIGURE 4.6 The relationship between KFI and % DM of marrow from the metacarpus of male (asterisk) and female (closed circle) bushbuck.

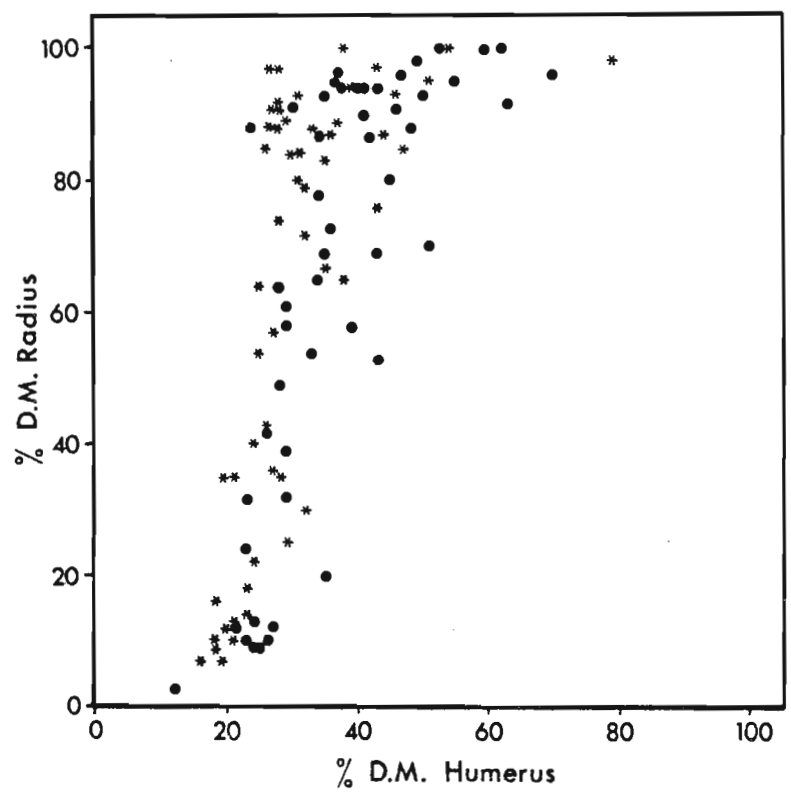


FIGURE 4.7 The relationship between % DM of marrow from the humerus and % DM of marrow from the radius of male (asterisk) and female (closed circle) bushbuck.

illustrated in Fig. 4.8 and may be described by the regression formulae:

male bushbuck: $y=0,957 + 0,956x$ ($r=0,939$; $p<0,001$)

female bushbuck: $y=0,834 + 0,953x$ ($r=0,924$; $p<0,001$)

where y=% DM of the metacarpus and x=% DM of the radius. Although scatter is more evident in the intermediate values from both bones, these results suggest that fat is mobilized from both the radius and the metacarpus at an approximately equal rate. This finding is supported by the fact that of the 106 animals from which all three bones were collected, 42% had highest % DM values from the metacarpus and lowest % DM values from the humerus, while 37% had highest % DM from

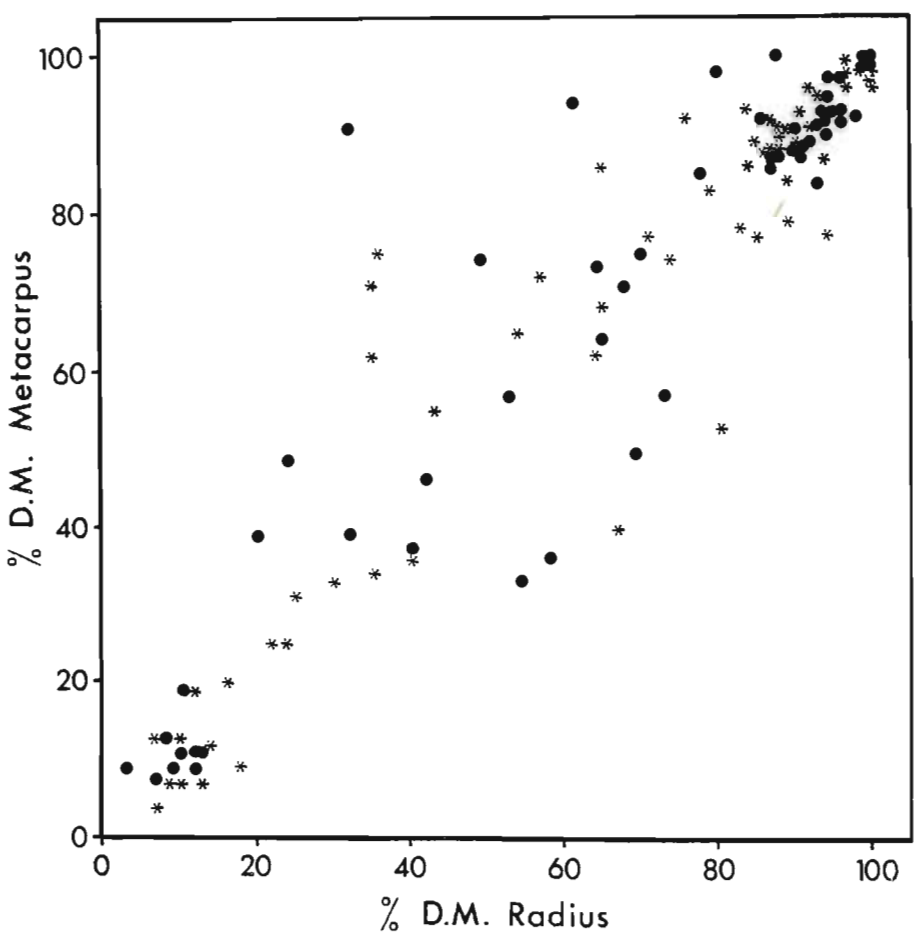


FIGURE 4.8 The relationship between % DM of marrow from the radius and % DM of marrow from the metacarpus of male (asterisk) and female (closed circle) bushbuck.

the radius, intermediate values from the metacarpus and lowest values from the humerus. In both of these groups, three animals (2,8%) had % DM values from all three bones of less than 50%. Five animals had highest % DM values recorded from the metacarpus, intermediate values from the humerus, and lowest values from the radius, and all of these bones had % DM values below 50%, while three of the animals had % DM values consistently below 30%. Only one bushbuck was found to have a highest % DM value from the radius and a lowest value from the metacarpus where all three bones were above 50% DM. The remaining bushbuck had highest values from the humerus and lowest values from either the metacarpus (8% of the sample) or radius (7%). In all of these remaining animals, none of the bones had a % DM higher than 30%. Overall, 26% of the bushbuck population sampled had % DM values from all three bones of less than 50%, while 18% of the bushbuck had all three bones with a % DM content of less than 30%.

An almost identical trend in the sequence of fat mobilization was evident in the duiker, with the exception that a higher proportion of animals had maximal % DM values from the metacarpus (Fig. 4.9). Consequently, the relationships between KFI and % DM of the humerus and radius, and between % DM of the humerus and the radius are not depicted graphically. As shown in Fig. 4.10, the % DM of the metacarpus did not decline until the KFI had fallen to a value of approximately 10. Although the relationships between % DM of the radius and metacarpus were essentially linear for both male and female duiker (Fig. 4.11), these relationships were not as good as for bushbuck. Nevertheless, they were equally significant and may be described by the following formulae:

male duiker: $y=15,181 + 0,776x$ ($r=0,657$; $p<0,001$)

female duiker: $y=4,055 + 0,892x$ ($r=0,627$; $p<0,001$)

where y=% DM of the carpus and x=% DM of the radius. These relationships indicate that fat is mobilized at a slightly

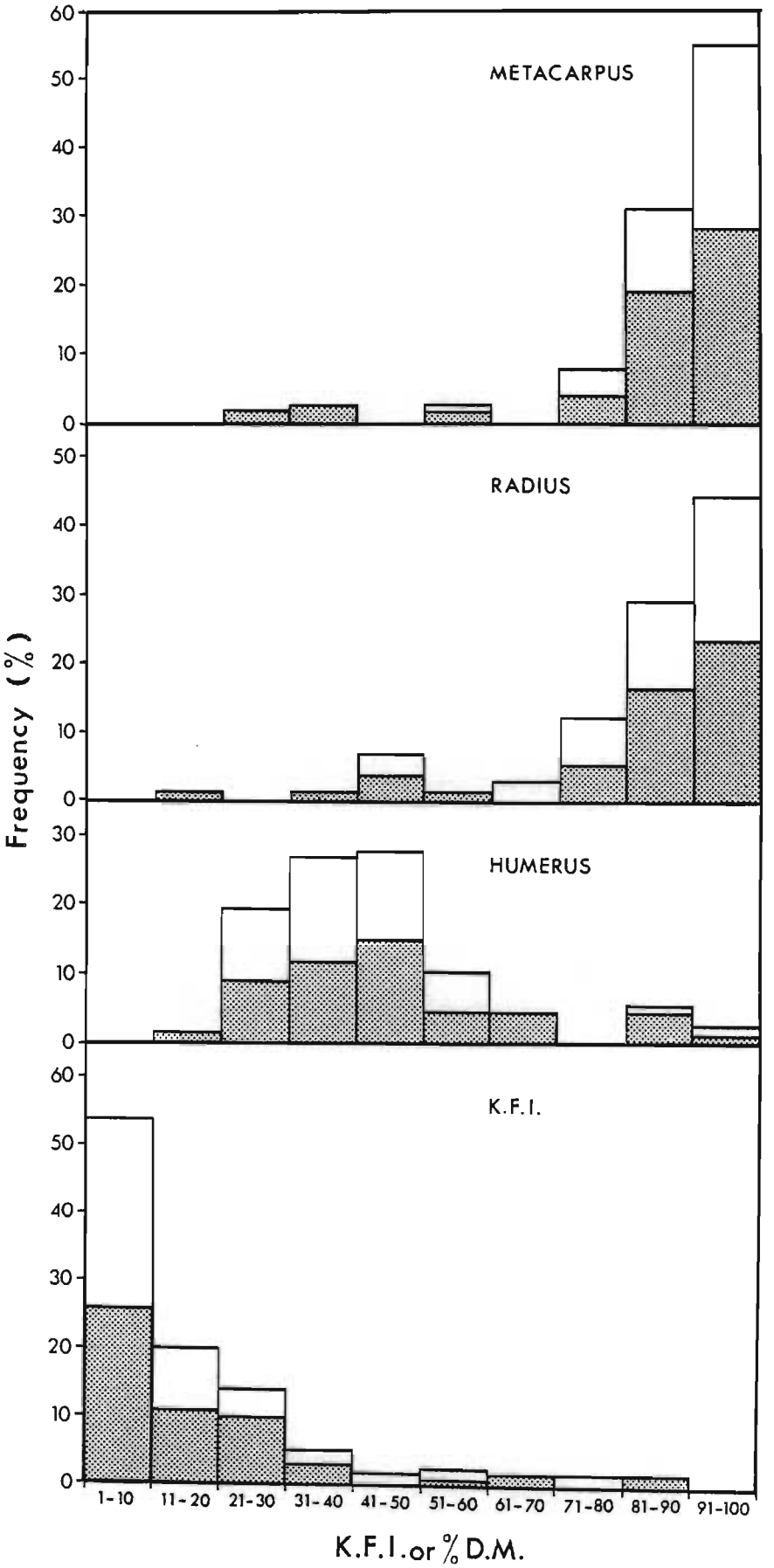


FIGURE 4.9 Frequency distribution of KFI and % DM values of bone marrow from duiker culled at Weza (shaded portion represents males).

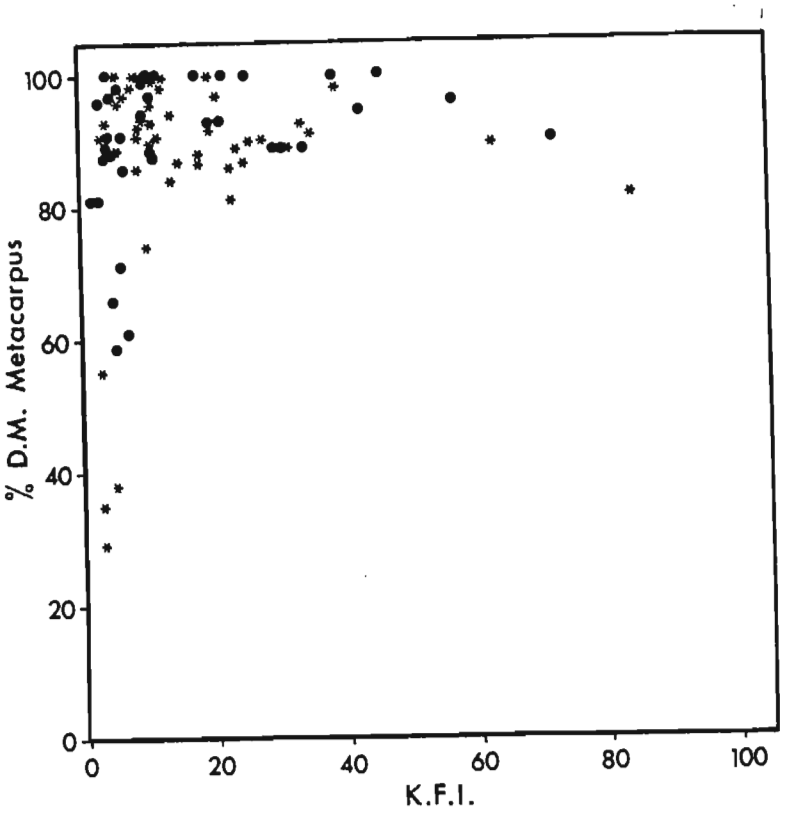


FIGURE 4.10 The relationship between KFI and % DM of marrow from the metacarpus of male (asterisk) and female (closed circle) duiker.

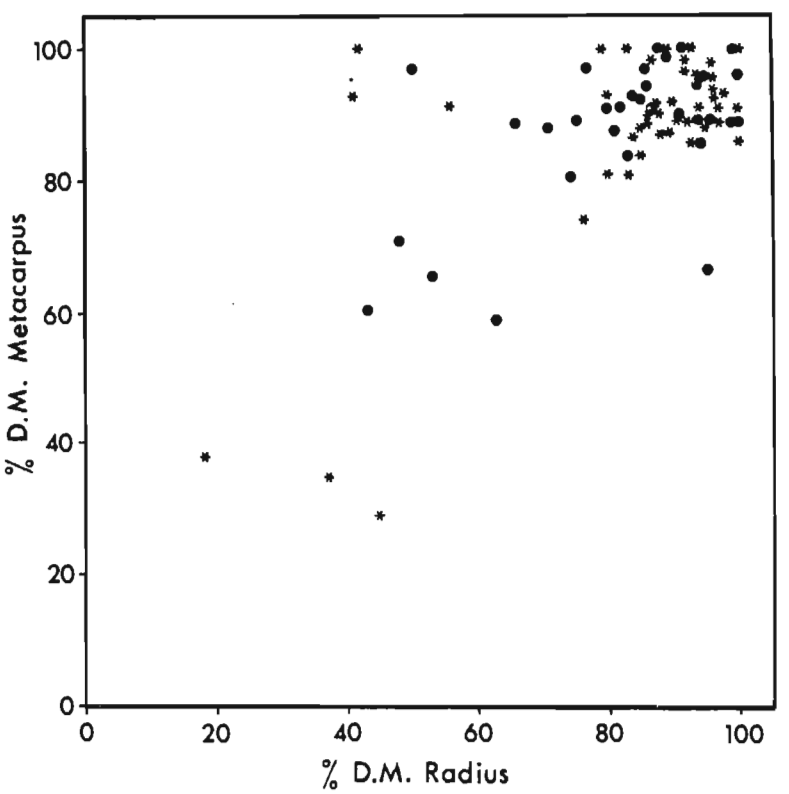


FIGURE 4.11 The relationship between % DM of marrow from the radius and % DM of marrow from the metacarpus of male (asterisk) and female (closed circle) duiker.

faster rate in the radius than in the metacarpus, and hence the sequential mobilization of fat proceeding distally from the proximal bone is more pronounced in this species than in the bushbuck. The fact that 60% of the 62 duiker from which all three bones were collected had highest % DM values in the metacarpus corroborates this conclusion. A further 34% of the duiker sample had highest % DM values recorded from the radius, intermediate values from the metacarpus and lowest values from the humerus, while the remaining 6% of the sample had highest % DM values from the radius and lowest values from the metacarpus. Only 5% of the sample had all three bones with % DM values under 50% and in contrast to bushbuck, none of the duiker examined had all three values consistently under 30%.

As a result of these findings, bone marrow data were not pooled but were treated independently in subsequent analyses of the relationships between age, sex and reproductive status and deposited fat reserves, and in seasonal and population comparisons, all of which are detailed below.

4.3.4 Fat Reserves of the Bushbuck

4.3.4.1 Sex differences in fat reserves

Although there were no significant differences between the KFI's of subadult males and females, adult male bushbuck had significantly lower KFI's than adult females ($t=2,025$; $p<0,05$). Seasonal differences between males and females were not significant however. Since at least 98% of the adult females examined in this study were either pregnant and/or lactating (see Chapter Five), adult males were compared to females of differing reproductive status. Differences between the KFI's of males and lactating or pregnant and lactating females were insignificant, but males had significantly lower KFI's than pregnant, non-lactating females ($t=3,456$; $p<0,001$).

The % DM of marrow from the humerus was significantly

lower in adult males than adult females ($t=2,880$; $p<0,05$) and differences were most pronounced during autumn ($t=2,785$; $p<0,01$) and spring ($t=2,636$; $p<0,02$). The % DM values from the radius were similar for both sexes throughout the year, while males had significantly lower % DM values from the metacarpus during the winter months ($t=2,271$; $p<0,05$).

As a result of these obvious differences in the fat reserves of males and females, the sexes were treated independently in all subsequent analyses.

4.3.4.2 Fat reserves in relation to reproductive status

Pregnant, non-lactating females had significantly higher KFI's than pregnant and lactating females ($t=2,288$; $p<0,05$) but did not differ significantly from non-pregnant, lactating females. Similarly there were no significant differences between the KFI's from lactating and pregnant and lactating females (Fig. 4.12).

Lactating females consistently had lower % DM values than either pregnant, or pregnant and lactating females, and although these differences were not significant for values from the humerus (Fig. 4.13), values from the radius and metacarpus of lactating females were significantly lower than those of pregnant bushbuck ($t=3,149$; $p<0,01$; and $t=2,966$; $p<0,01$, respectively, see Figs. 4.12 and 4.13). Condition indices from pregnant females generally differed only slightly from those obtained from one female that was neither visibly pregnant nor lactating (Figs. 4.12 and 4.13).

Since there is no fixed breeding season in the bushbuck (see Chapter Five), possible variation of KFI during gestation was also examined. Fig. 4.14 shows that KFI's were highest during the later stages of pregnancy at a time when nutritional demands (with respect to pregnancy) would be greatest. This apparently anomalous relationship may however be explained by the fact that all except one of the females with KFI's higher than 30 were collected during the summer

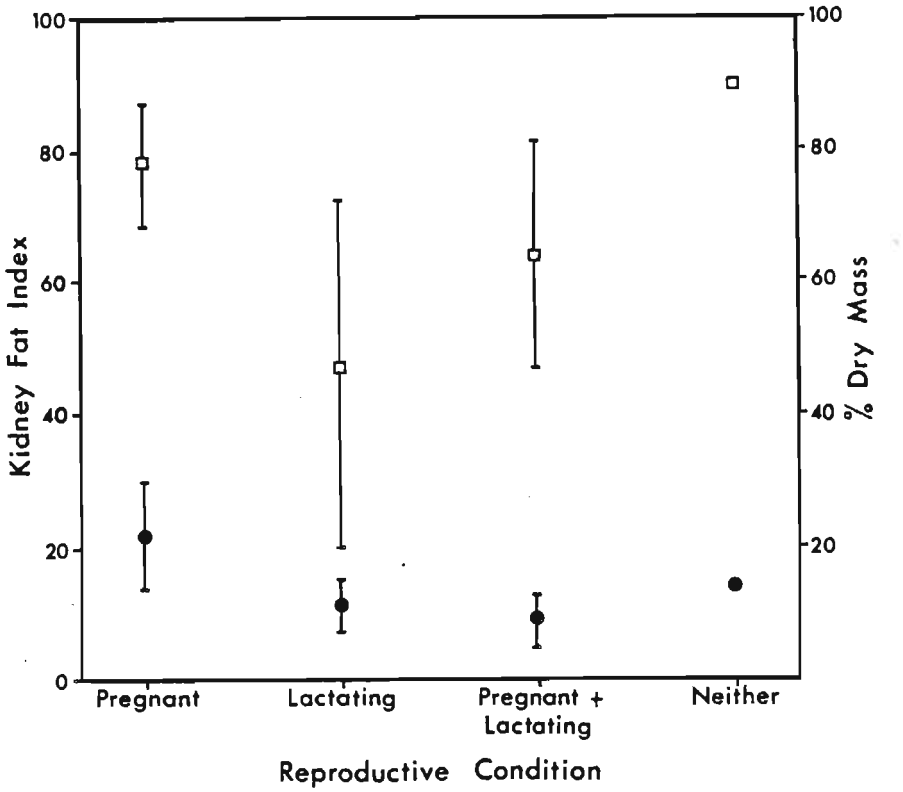


FIGURE 4.12 Variation in deposited fat reserves of female bushbuck in relation to reproductive status (closed circle - KFI; open square - % DM of metacarpus; means ± 2 standard errors are shown).

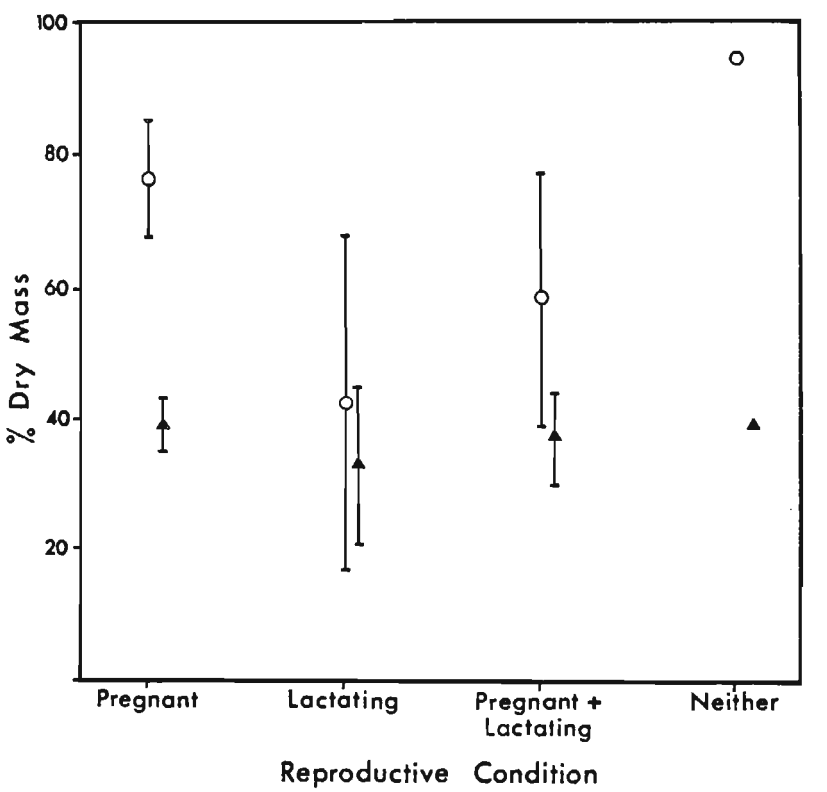


FIGURE 4.13 Variation in deposited fat reserves of female bushbuck in relation to reproductive status (closed triangle - % DM of humerus; open circle - % DM of radius; means ± 2 standard errors are shown).

and autumn months. Consequently, these higher indices may reflect seasonal rather than reproductively-induced influences. In addition, none of these females were actively nursing an infant (the two females with full term foetuses in Fig. 4.14 were producing colostrum) and therefore were not subject to the additional energetic demands of lactation.

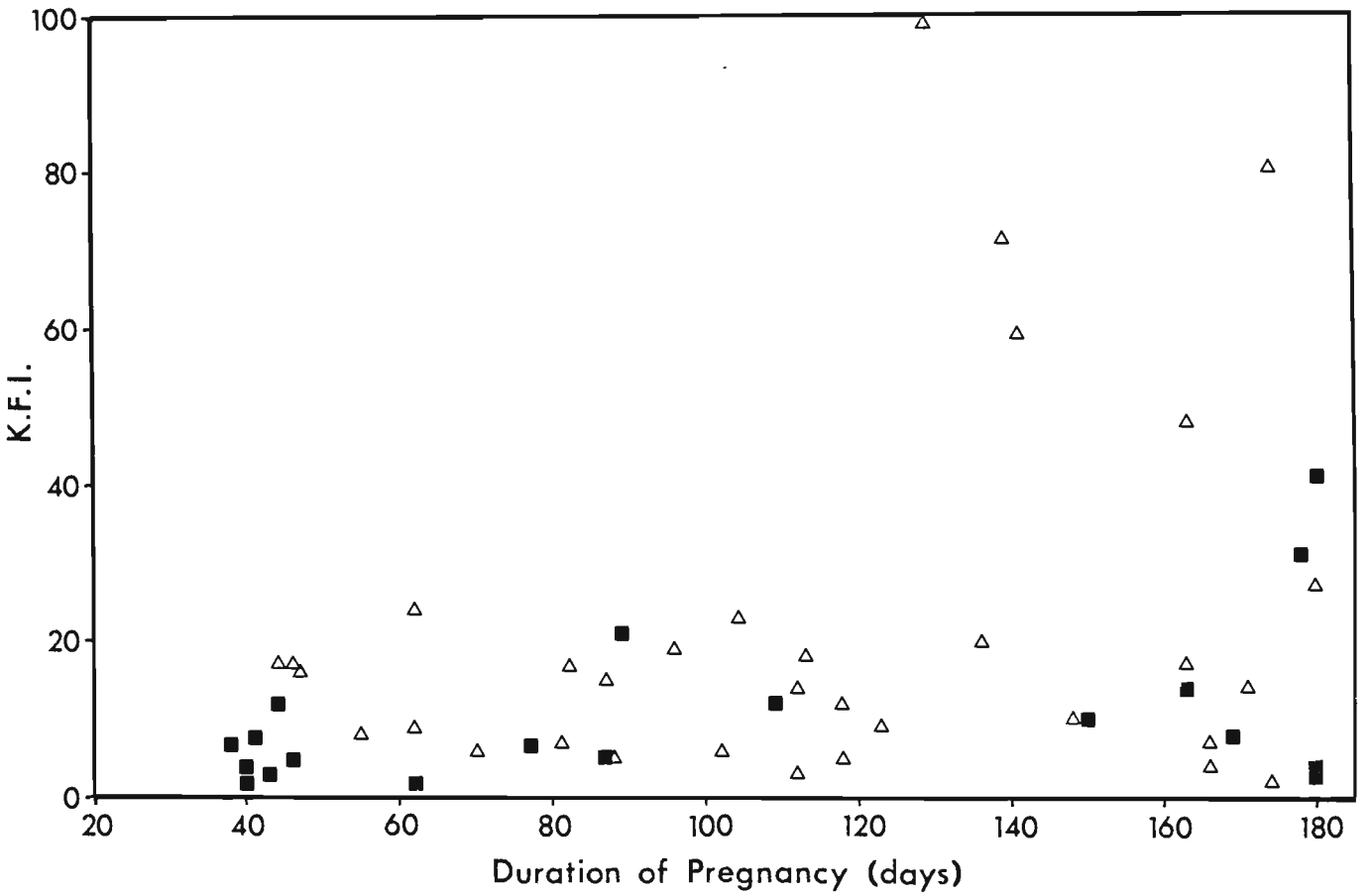


FIGURE 4.14 Variation in KFI values with duration of pregnancy in female bushbuck (open triangle - pregnant, non-lactating; closed square - pregnant and lactating).

4.3.4.3 Fat reserves in relation to age

Mean KFI and % DM values for subadults and adults are summarized in Table 4.1 and 4.2 for male and female bushbuck respectively. While the KFI's from juvenile males (1-12 months) did not differ from those of adult males, KFI's from yearling males were significantly lower than those from adults ($t=2,478$; $p<0,01$). The mean KFI obtained from all

subadult males under 30 months of age was also significantly lower than that of adult males (t=2,817; p<0,01). Yearling and subadult males also had lower KFI's than 48 month old males, (t=3,873; p<0,001 and t=3,013; p<0,01 respectively) but differences between the KFI's from all other age classes were not significant.

The % DM values of all three bones from subadults did not differ markedly from those of adult males, but the values obtained from the humerus, radius and metacarpus of 48 month old males were consistently greater than those from 156 month old animals (t=2,242; p<0,05; t=3,066; p<0,02 and t=2,368; p<0,05 respectively). Differences resulting from all other age specific comparisons were not significant.

TABLE 4.1 Variation in fat reserves with age in male bushbuck.

Age class (in months)		KFI	% DM of:		
			Humerus	Radius	Metacarpus
Juveniles (1 - 12)	n	7	5	5	5
	Mean	7,76	24,05	54,90	52,50
	S.E.	1,26	6,47	9,61	11,25
Yearlings (13 - 26)	n	7	3	3	3
	Mean	5,69	28,20	56,23	68,9
	S.E.	0,62	4,37	16,59	11,57
All subadults (0 - 26)	n	14	8	8	8
	Mean	6,72	25,62	55,38	56,85
	S.E.	0,74	4,19	7,91	8,28
Adults (30 +)	n	66	57	61	61
	Mean	11,31	30,80	63,93	65,77
	S.E.	0,73	1,45	4,07	4,00

The use of total body mass as an index of condition was limited by age-specific differences in male bushbuck. As might be expected from the growth pattern of this species (see Chapter Three), 72 month old males were significantly heavier than 48 month old animals (t=2,652; p<0,02) while 96 month old males were significantly heavier than 132 month old individuals (t=2,097; p<0,05). All other age-specific differences in total body mass were not significant.

TABLE 4.2 Variation in fat reserves with age in female bushbuck.

Age class (in months)		KFI	% DM of:		
			Humerus	Radius	Metacarpus
Juveniles (1 - 12)	n	6	3	3	3
	Mean	8,22	31,07	60,60	66,87
	S.E.	0,60	5,96	21,10	15,96
Yearlings (13 - 26)	n	11	4	6	6
	Mean	11,39	40,12	78,34	81,55
	S.E.	3,23	9,53	9,12	8,29
All subadults (0 - 26)	n	17	7	9	9
	Mean	10,27	36,25	72,43	76,65
	S.E.	2,09	5,87	8,99	7,47
Adults (30 +)	n	60	51	53	54
	Mean	16,27	37,23	64,95	67,89
	S.E.	2,44	1,72	4,52	4,34

Fat reserves of female bushbuck showed much less variation with age, and although the oldest adults exhibited the same trend as the oldest males in that their fat reserves were consistently lower than those from all other adults (see Figs. 4.15 and 4.16), none of these differences were

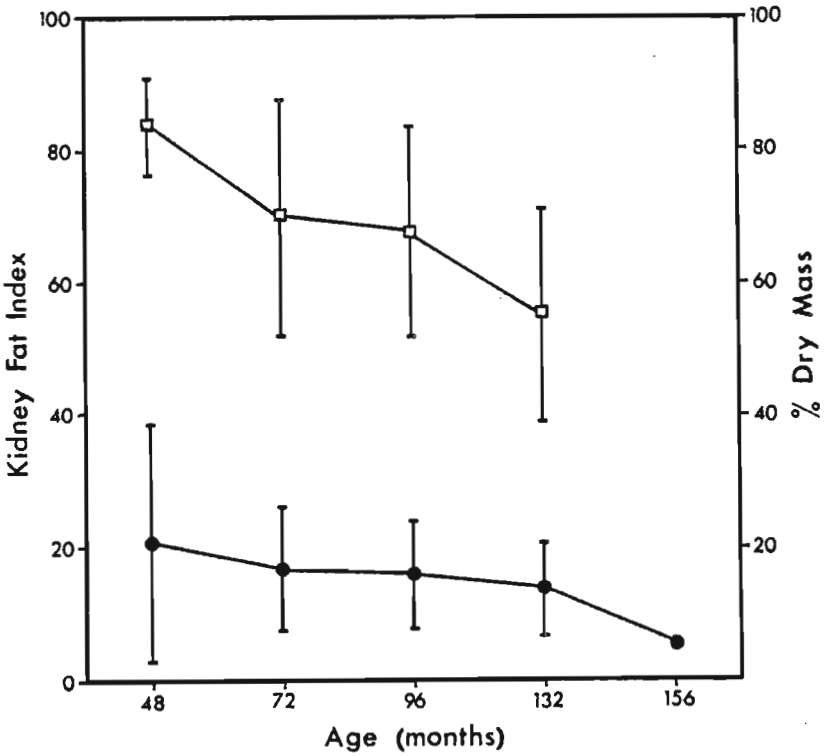


FIGURE 4.15 The relationship between age and deposited fat reserves of adult female bushbuck (closed circle - KFI; open square - % DM of metacarpus; means ± 2 standard errors are shown).

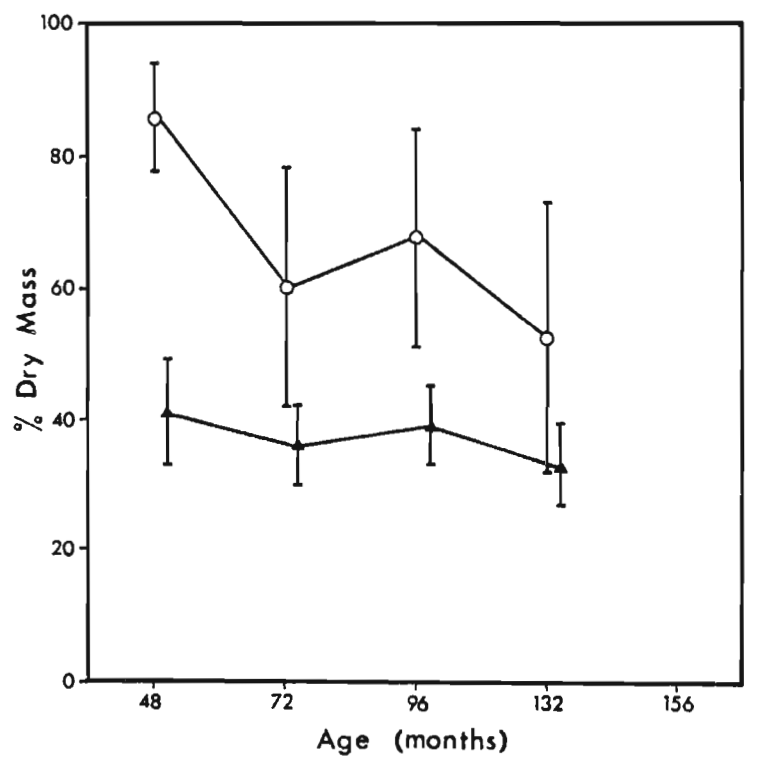


FIGURE 4.16 The relationship between age and deposited fat reserves of adult female bushbuck (closed triangle - % DM of humerus; open circle - % DM of radius; means ± 2 standard errors are shown).

significant. In additions, there were no significant differences between juveniles, yearlings, subadults and adults in all of the condition indices that were examined.

Since these results demonstrate that fat reserves of male bushbuck varied with age, seasonal comparisons were confined to data from adults only. Although the effect of age on physiological condition was not as pronounced in females, for comparative purposes seasonal analyses were also restricted to the adult segment of the culled sample.

4.3.4.4 Fat reserves in relation to season

Both adult males and adult females showed well defined annual cycles of condition. Fluctuations in % DM from all three bones followed a similar trend, and were consistently highest during the winter months, and at their lowest values during spring. Both male and female KFI's were also lowest during the spring, but highest in the summer. Maximal perinephric fat reserves were therefore six months out of phase with maximal marrow fat reserves, presumably as a result of sequential mobilization and lipogenesis. The amplitudes of these seasonal changes in fat reserves are illustrated for females in Figs. 4.17 and 4.18, while seasonal variations in male condition are not depicted since they follow an identical trend.

Significant seasonal differences were evident in every condition parameter examined for both sexes, and have consequently been summarized in Appendix B (Tables B.1 to B.4 and B.5 to B.8 for males and females respectively). Both male and female KFI's were significantly lower in spring than in summer (Tables B.1 and B.5) while their % DM values from all bones were significantly and consistently lower in spring when compared to the winter months (Tables B.2 to B.4 and B.6 to B.8).

Despite the obvious age-related changes detailed above, adults males exhibited pronounced seasonal variations in

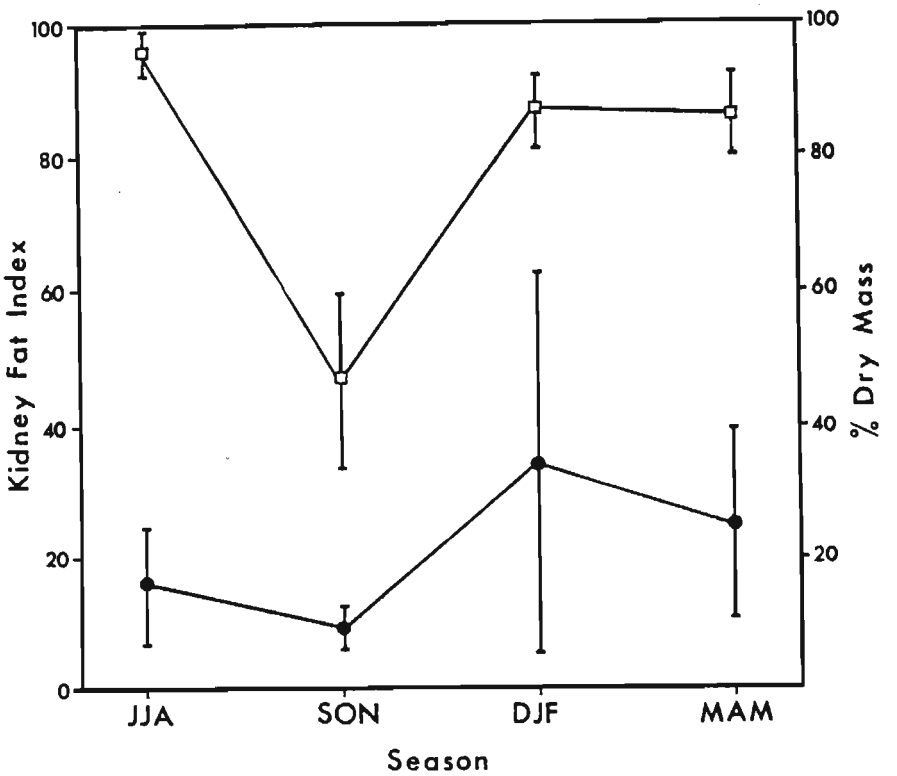


FIGURE 4.17 Seasonal changes in the deposited fat reserves of adult female bushbuck (closed circle - KFI; open square - % DM of metacarpus; means ± 2 standard errors are shown).

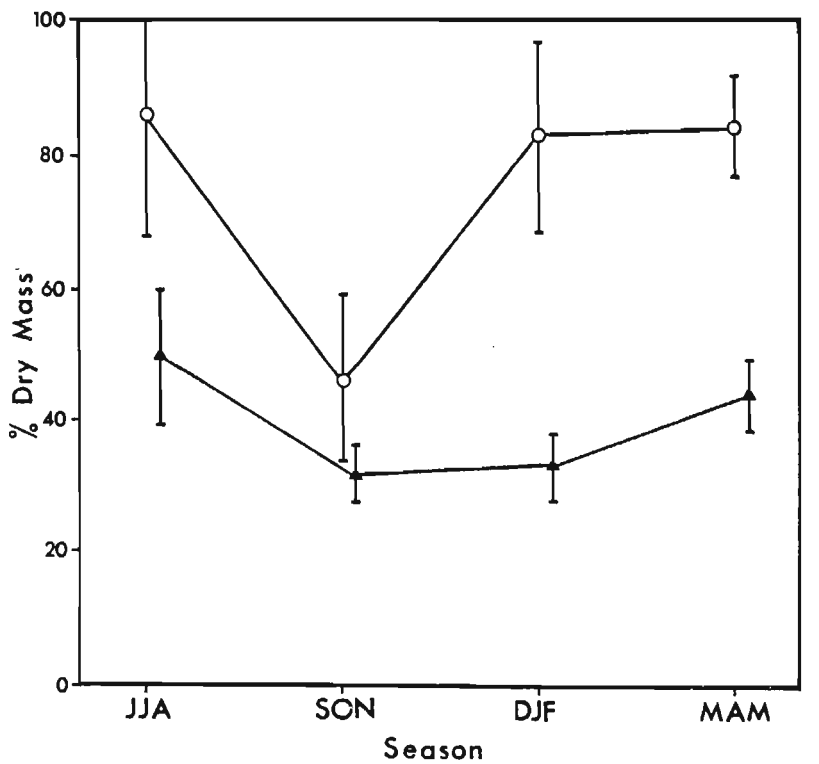


FIGURE 4.18 Seasonal changes in the deposited fat reserves of adult female bushbuck (closed triangle - % DM of humerus; open circle - % DM of radius; means ± 2 standard errors are shown).

total body mass which corresponded to changes in % DM values. These are summarized in Appendix B, Table B.9.

4.3.4.5 Fat reserves in relation to management

Comparisons between the condition data obtained from the Weza population and from bushbuck hunted on surrounding farms were confined to adult males collected in winter months (i.e. during the hunting season). Males from farms had significantly higher KFI's than male bushbuck from Weza at this time ($t=2,521$; $p<0,02$) but the % DM values from the metacarpus of all males from both areas were similar. However, 48 month old males from farmland had higher % DM values than their peers at Weza ($t=2,194$; $p<0,05$) at the time of the year when % DM values were highest (see above), but all other age-specific differences in condition indices were not significant.

Adult males from Weza were significantly heavier than farm bushbuck during the winter months ($t=2,605$; $p<0,02$). Although these results initially appear to be contradictory when compared to differences in fat reserves, the age structure of the males hunted on farms and culled at Weza differed markedly, with a much higher proportion of younger males harvested on farmland (Fig. 4.19). However, all age-specific differences in body mass were not significant at this time of the year.

4.3.5 Fat Reserves of the Duiker

4.3.5.1 Sex differences in fat reserves

Fat reserves of males did not differ significantly from those of female duiker at any time of the year, between specific age classes (including subadults) or with respect to female reproductive status.

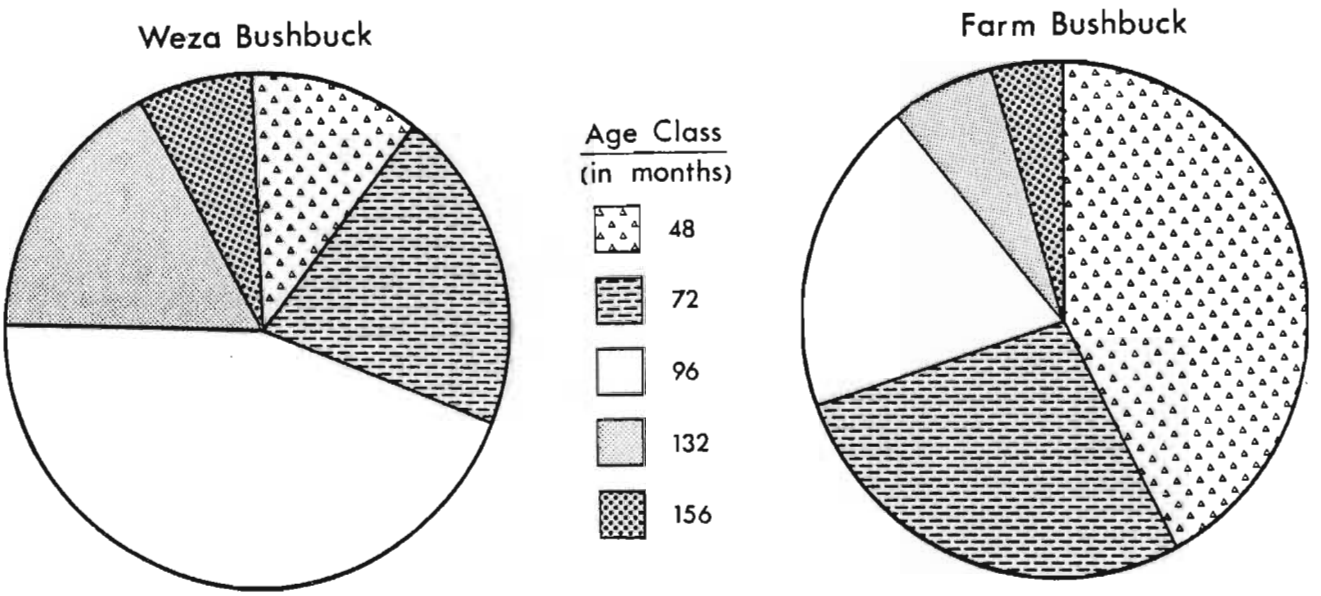


FIGURE 4.19 The age structure of adult male bushbuck culled at Weza (n=59) and hunted on neighbouring farms (n=47).

4.3.5.2 Fat reserves in relation to reproductive status

Reproductive status had little influence on KFI and % DM values from the humerus, but pregnant, not lactating females had significantly higher % DM values from the radius and metacarpus when compared to pregnant and lactating females ($t=3,964$; $p<0,001$ and $t=2,156$; $p<0,05$ respectively, see Figs. 4.20 and 4.21). One adult female that was neither visibly pregnant nor lactating had a lower KFI than reproductively active females, while the % DM values recorded from this animal were similar (from the humerus) or higher (from the radius and metacarpus) than those obtained from pregnant and lactating females (Figs. 4.20 and 4.21).

Pregnant female duiker had higher perinephric fat reserves during the latter two thirds of gestation, and none of the pregnant females with KFI's higher than 30 were actively nursing an infant, while one of these females with a nearly full term foetus was producing colostrum (Fig. 4.22). With the exception of this latter female that was collected in February, all of these females with KFI's above 30 were

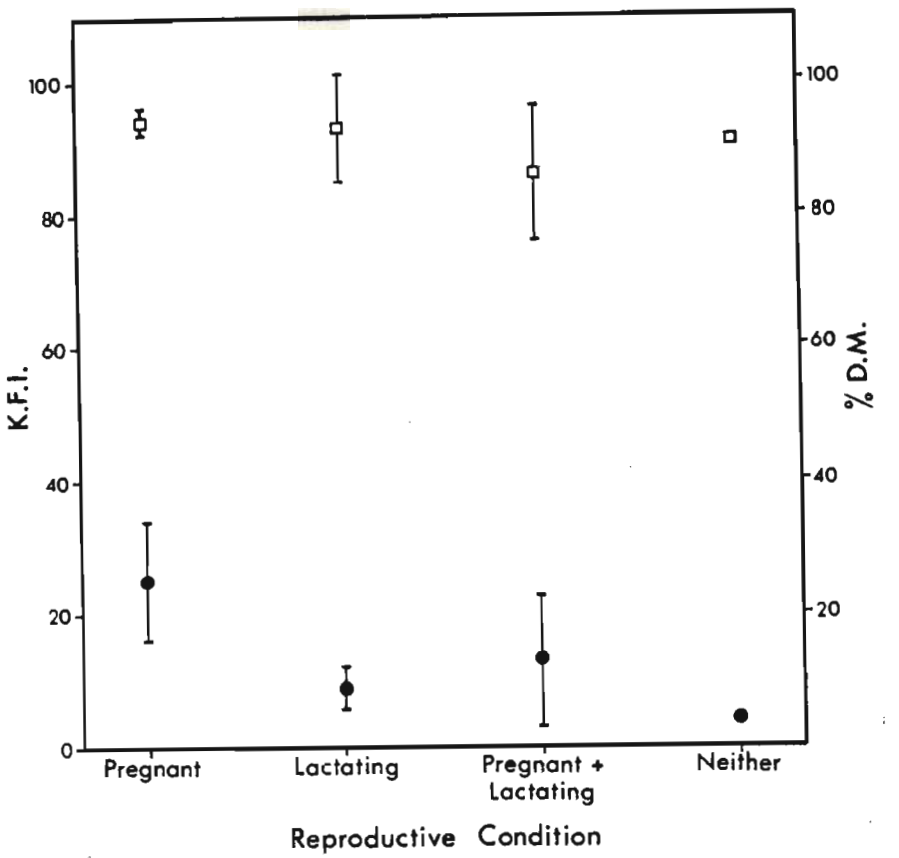


FIGURE 4.20 Variation in deposited fat reserves of female duiker in relation to reproductive status (closed circle - KFI; open square - % DM of metacarpus; means ± 2 standard errors are shown).

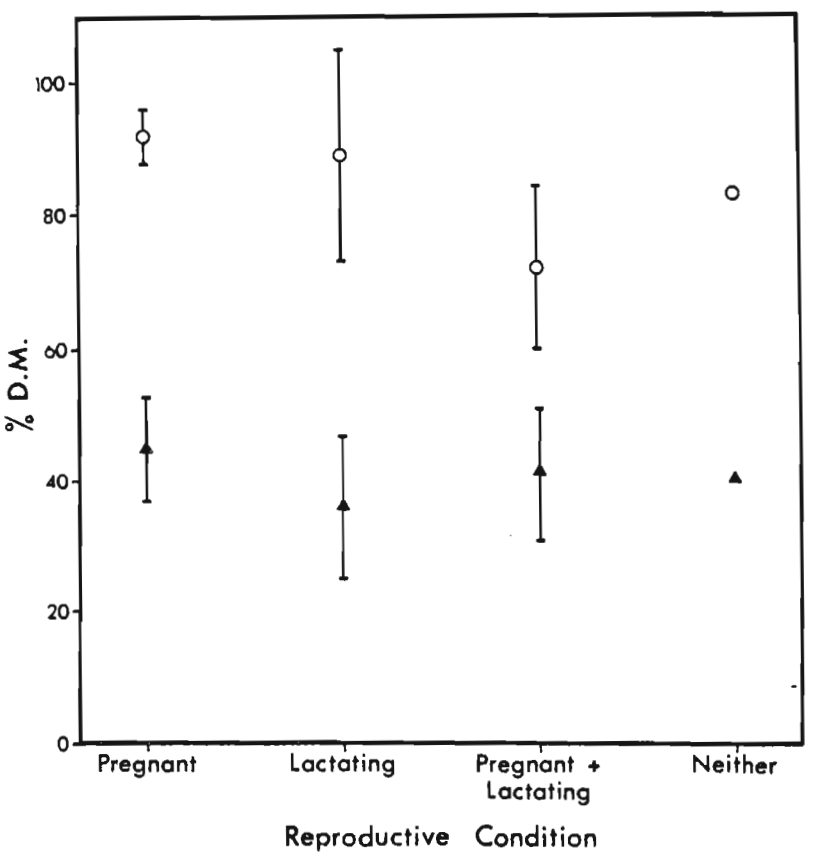


FIGURE 4.21 Variation in deposited fat reserves of female duiker in relation to reproductive status (closed triangle - % DM of humerus; open circle - % DM of radius; means ± 2 standard errors are shown).

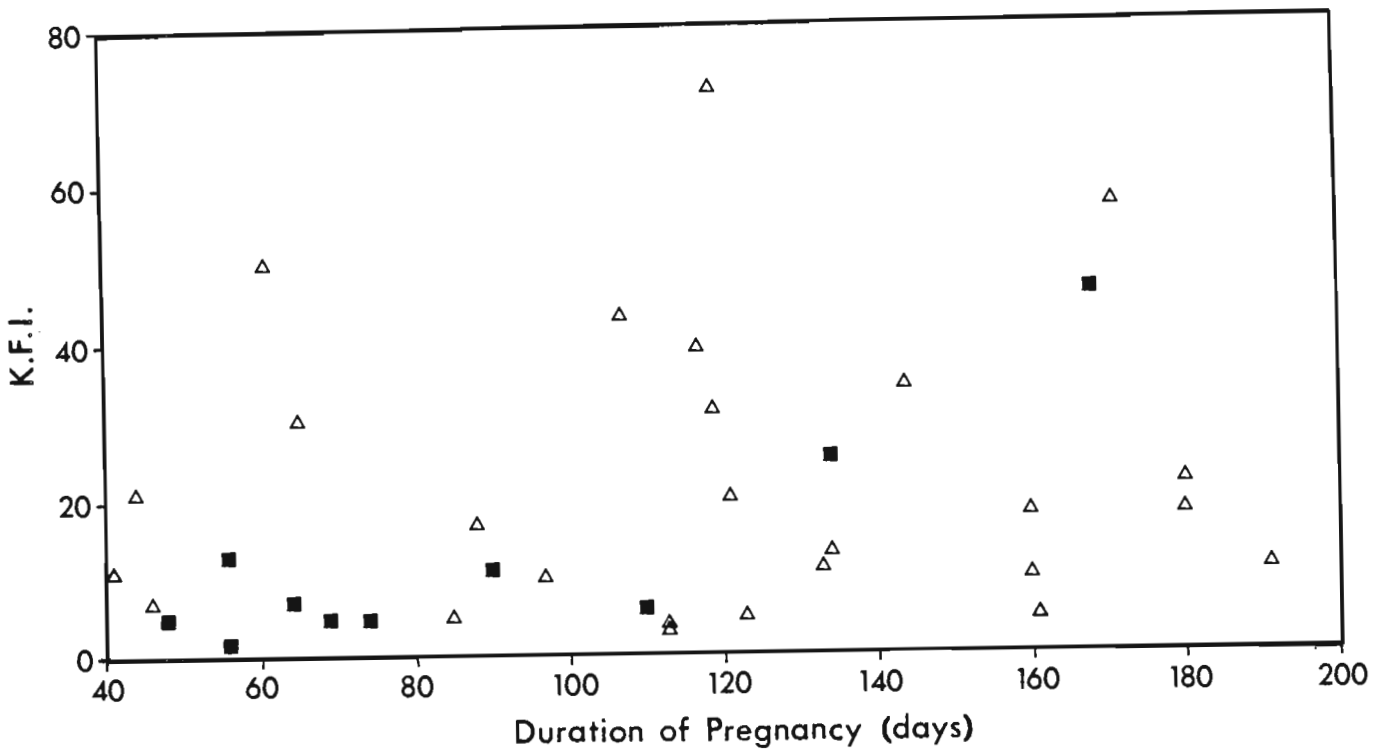


FIGURE 4.22 Variation in KFI values with duration of pregnancy in female duiker (open triangle - pregnant, non-lactating; closed square - pregnant and lactating).

culled during the autumn and winter months, when perinephric fat reserves, irrespective of reproductive status, were higher than the remainder of the year (see below).

4.3.5.3 Fat reserves in relation to age

Mean KFI and % DM values for subadults and adults are summarized in Tables 4.3 and 4.4 for male and female duiker respectively. Differences in KFI values from male juveniles (1-9 months), yearlings (10-19 months) and all subadults (1-19 months inclusive) were not significant when compared to KFI's from adult males. Inadequate samples precluded comparisons of % DM values between juvenile and adult males, while yearling males and all subadults had values generally lower (but not significantly so) than those of adult males. None of the age-specific differences in condition indices were significant among adults males, with the one exception that 168 month old duiker were significantly heavier than 20 month old males ($t=4,041$; $p<0,001$).

TABLE 4.3 Variation in fat reserves in male duiker.

Age class (in months)		KFI	% DM of:		
			Humerus	Radius	Metacarpus
Juvenile (1 - 9)	n	6	2	3	3
	Mean	5,49	28,64	72,67	73,56
	S.E.	0,59	-	12,48	14,28
Yearling (10 - 19)	n	9	5	5	5
	Mean	13,39	36,36	89,87	91,23
	S.E.	2,47	6,85	2,34	2,56
All subadults (1 - 19)	n	15	7	8	8
	Mean	10,23	34,15	83,42	84,61
	S.E.	1,79	4,94	5,34	5,89
All adults (20 +)	n	48	34	39	41
	Mean	18,24	45,50	82,45	86,41
	S.E.	2,36	3,13	3,15	2,65

Almost identical trends were evident from similar comparisons between females of differing age, and although adult female condition indices were consistently higher than those obtained from all subadult female duiker, differences were significant only between the % DM of the metacarpus from subadults when compared to the same parameter in adults ($t=3,825$; $p<0,001$). Both juveniles and yearling female duiker had significantly lower % DM metacarpus values than adults ($t=3,875$; $p<0,001$ and $t=2,690$; $p<0,02$ respectively). Age-specific differences were not evident among adult female fat reserves.

As a consequence of these age-related differences in condition, seasonal comparisons of fat reserves on both males and females were confined to duiker at least 20 months old.

TABLE 4.4 Variation in fat reserves in female duiker.

Age class (in months)		KFI	% DM of:		
			Humerus	Radius	Metacarpus
Juvenile (1 - 9)	n	11	3	4	4
	Mean	15,61	40,59	77,55	71,61
	S.E.	6,38	11,60	11.31	8,10
Yearling (10 - 19)	n	9	7	8	8
	Mean	9,26	30,73	76,52	81,17
	S.E.	1,92	3,67	6,68	5,00
All subadults (1 - 19)	n	20	10	12	12
	Mean	12,75	33,69	76,86	77,98
	S.E.	3,61	4,19	5.53	4,29
All adults (20 +)	n	36	32	33	33
	Mean	18,49	42,42	86,08	92,00
	S.E.	2,92	2,70	2,47	1,59

4.3.5.4 Fat reserves in relation to season

In contrast to bushbuck, both male and female duiker from Weza had most extensive reserves of perinephric fat during the autumn months. This species resembled bushbuck however in that perinephric fat reserves were most depleted during the spring, and for males, these were significantly lower than in winter ($t=4,496$; $p<0,001$), summer ($t=2,755$; $p<0,02$), or during the entire year ($t=2,535$; $p<0,02$). Female KFI values were significantly lower in spring than in winter ($t=2,585$; $p<0,02$) but not during any other time of the year.

Both male and female duiker also resembled bushbuck in that % DM values from all three bones were highest in winter, but seasonal differences in these values were not significant at any time of the year in males, while the only significant difference in females involved the % DM values of the

metacarpus which were higher in summer than in autumn ($t=2,571$; $p<0,05$).

4.3.5.5 Fat reserves in relation to management

Because of the small sample of adult duiker (n=13) harvested on surrounding farms, male and female data were pooled for comparisons between populations at Weza and on farmland. Although perinephric fat reserves in farm duiker were on average twice as high as those from duiker at Weza (mean values of 40,5 + 11,8 and 23,7 + 3,7 respectively) this difference was not significant due to the considerable variability (ranging from 10,5 to 165,6) in KFI's from the former population. Non-significant differences were also evident in % DM metacarpus values and in total body mass values of adult males.

4.3.6 Adrenocortical Hypertrophy

4.3.6.1 Duiker

The adrenal glands of the duiker are both situated in a suprarenal position. The left kidney and its associated adrenal are situated posterior to their right counterparts, and are clearly separated from the vena cava and the liver. The left adrenal is firmly attached to the anterior pole of the kidney, and is relatively easy to locate. In contrast, the right adrenal and the kidney are closer to the mid-line, and the adrenal itself is close to the vena cava and covered by the lower lobes of the liver, to which it adheres (Allen-Rowlandson *et al.* (in prep.)).

In 78 of the 99 duiker in which both adrenal glands were weighed, the left adrenal was heavier than the right, and in the total sample of 99 this difference was highly significant ($t=5,849$; $p<0,001$).

Growth in combined adrenal mass with age in male and female duiker is shown in Table 4.5. Although there was

considerable variation in mass with age, the adrenals in male duiker probably reached their asymptote of mass increase at about 10 months, whereas the adrenals of females continued growing throughout life. From at least 60 months of age and onwards, the adrenals of female duiker were significantly heavier than those of males, and in duiker over 120 months, this difference was highly significant (Table 4.5).

TABLE 4.5 Growth in combined adrenal mass with age in male and female duiker.

Age (months)	Sex	n	Mean combined adrenal mass (g) ± S.E.	t value and level of significance
3 - 7	M F	5 10	0,532 ± 0,037 0,684 ± 0,065	1,567 n.s.
9 - 10	M F	7 7	0,846 ± 0,086 0,774 ± 0,038	0,767 n.s.
20	M F	8 7	0,738 ± 0,034 0,832 ± 0,037	1,874 n.s.
60	M F	8 5	0,815 ± 0,063 1,008 ± 0,031	2,2288 p<0,05
84	M F	10 8	0,772 ± 0,032 1,092 ± 0,081	3,983 p<0,01
120-180	M F	9 11	0,807 ± 0,042 1,248 ± 0,067	5,287 p<0,001

Female duiker were generally larger than male duiker of equivalent age, and thus the higher adrenal mass of the female duiker might be related to body size per se and not to a relative increase in the quantity of adrenal tissue. Thus for comparative purposes, the change in adrenal index with

age is shown in Table 4.6, where the adrenal index is calculated as mg of adrenal gland/100g of body weight.

TABLE 4.6 Variation in adrenal index with age in male and female duiker.

Age (months)	Sex	n	Adrenal index ± S.E.	t value and level of significance
3 - 7	M	5	6,40 ± 0,24	0,375
	F	8	6,64 ± 0,47	n.s.
9 - 10	M	6	5,86 ± 0,71	0,429
	F	8	6,15 ± 0,27	n.s.
20	M	8	5,29 ± 0,24	0,226
	F	7	5,38 ± 0,33	n.s.
60	M	8	5,92 ± 0,40	0,444
	F	5	6,17 ± 0,31	n.s.
84	M	10	5,27 ± 0,14	2,164
	F	7	6,56 ± 0,69	p<0,05
120-180	M	9	5,37 ± 0,21	3,282
	F	10	7,37 ± 0,54	p<0,01

In all the age classes, females had a higher adrenal index, although the difference was significant only in the older animals (Table 4.6). On the assumption that the heavier adrenals would have a higher cortex/medulla ratio, the duiker adrenals were examined histologically in relation to age and sex (Table 4.7). Although the older female duiker had on average a higher cortex/medulla ratio than male duiker of the same age, the difference was significant in only one age group.

TABLE 4.7 Variation in cortex/medulla ratio with age in male and female duiker.

Age (months)	Sex	n	C.M. ratio ± S.E.	t value and level of significance
3 - 7	M F	5 9	2,606 ± 0,801 2,908 ± 0,164	0,886 n.s.
9 - 10	M F	7 7	2,807 ± 0,399 3,117 ± 0,262	0,648 n.s.
20	M F	7 7	2,681 ± 0,269 2,215 ± 0,145	1,521 n.s.
60	M F	6 5	2,410 ± 0,340 2,486 ± 0,196	0,182 n.s.
84	M F	9 9	2,338 ± 0,188 2,960 ± 0,184	2,355 p<0,05
120-180	M F	10 13	2,389 ± 0,294 2,868 ± 0,246	1,251 n.s.

There was no correlation between adrenal mass and cortex/medulla ratio, but if adrenal mass was corrected for body size through the use of the adrenal index, the cortex/medulla ratio is significantly correlated in both males and females (Figs. 4.23 and 4.24). Information on the adrenals were collected from five male mortalities, and the relevant data are marked in Fig. 4.23. The one animal clearly separated from the whole sample is duiker No. 80, a nine month old found dead in a snare which had the highest cortex/medulla ratio of all the males (4.94) and the highest adrenal index (9,28). The KFI was 8,3. In the absence of information on the quantity and quality of social interactions in the duiker studied, the cause of the obvious adrenocortical hypertrophy of duiker No. 80 remains open to

speculation. Only two females that had recently died were found, and the one from which adrenal material was collected is marked in Fig. 4.24. The adrenocortical hypertrophy in the females is almost certainly related to hormonal changes during oestrus, pregnancy and lactation.

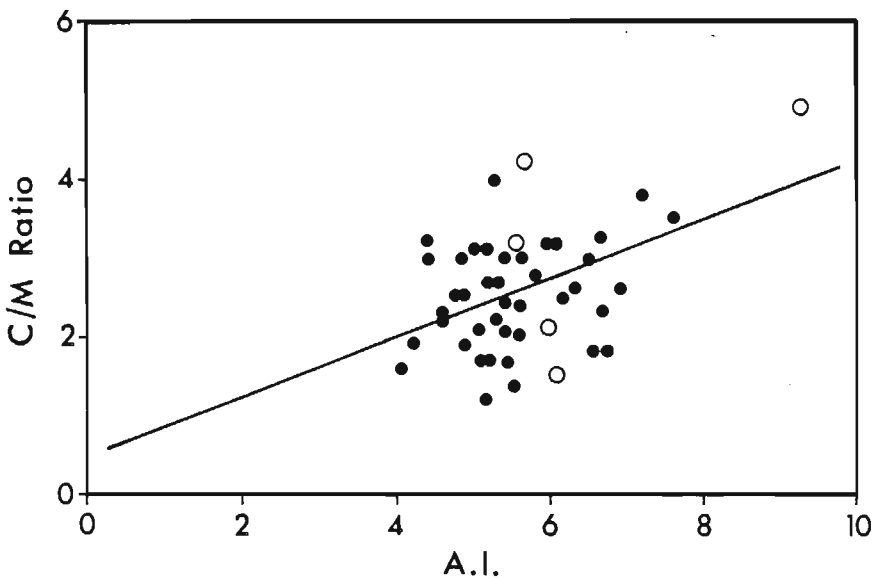


FIGURE 4.23 The relationship between cortex/medulla ratio and adrenal index in male duiker (open circle - mortality); $y = 0,482 + 0,374x$ ($r=0,448$; $p<0,05$).

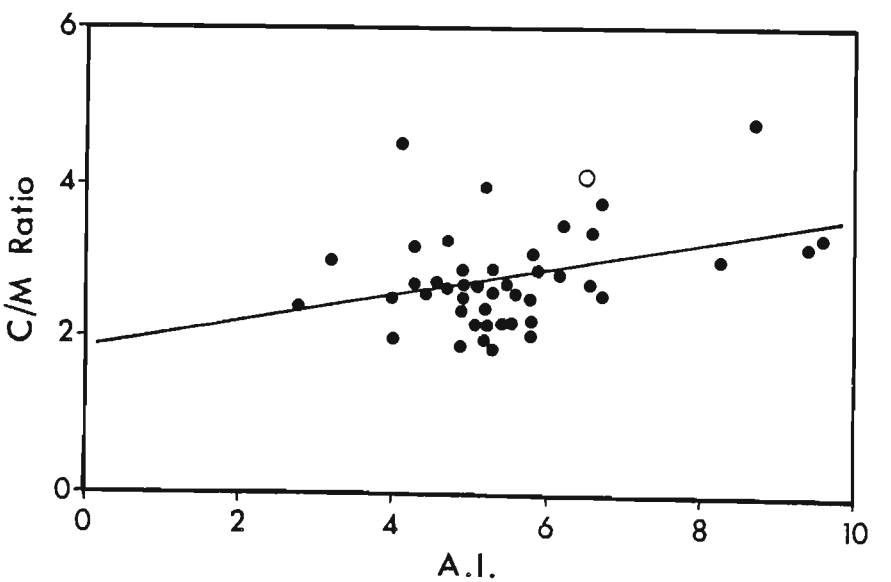


FIGURE 4.24 The relationship between cortex/medulla ratio and adrenal index in female duiker (open circle - mortality); $y = 1,667 + 0,174x$ ($r=0,368$; $p<0,05$).

There was no correlation between the adrenal index and KFI in the duiker (Figs. 4.25 and 4.26), nor was there any correlation between adrenal index and % DM values from bone marrows.

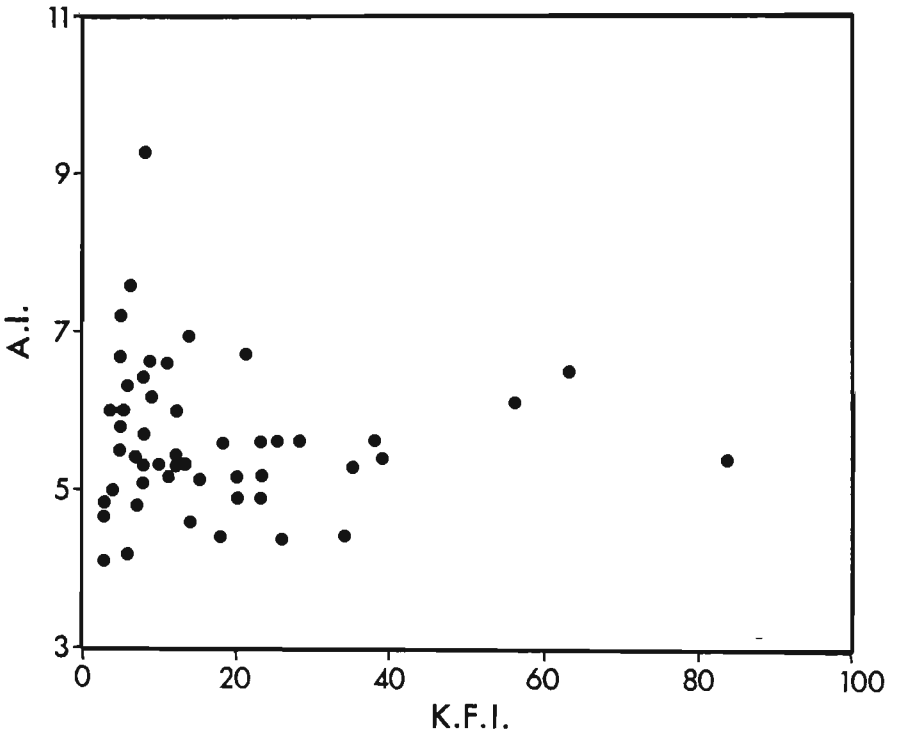


FIGURE 4.25 The relationship between KFI and adrenal index in male duiker.

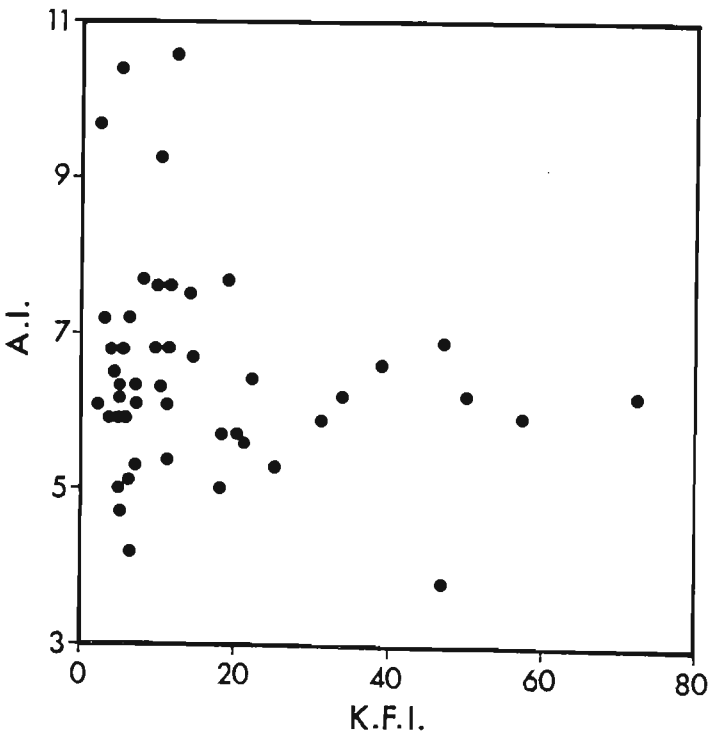


FIGURE 4.26 The relationship between KFI and adrenal index in female duiker.

4.3.6.2 Bushbuck

As in the duiker, the adrenal glands of the bushbuck are also situated in a suprarenal position in an almost identical location relative to the vena cava and the liver.

In 105 of the 127 bushbuck in which both adrenal glands were weighed, the left adrenal was heavier than the right, and in the total sample of 127 this difference was highly significant ($t=7,908$; $p<0,001$).

Growth in combined adrenal mass with age in male and female bushbuck is shown in Table 4.8. In contrast to the duiker, the adrenals of the male bushbuck were significantly heavier than those of the females in the majority of animals older than 21 months, and in bushbuck over 96 months, this difference was highly significant (Table 4.8). Unlike the duiker, the adrenals of female bushbuck do not appear to continue growing throughout life, reaching an asymptote between 48 and 72 months, male bushbuck probably reaching their asymptote of mass increase between 72 and 96 months.

Adult male bushbuck are taller and heavier than females of equivalent age, (Chapter Three), and thus for comparative purposes the change in adrenal index with age is shown in Table 4.9 and in Figs. 4.27 and 4.28. Like the duiker, the females generally have relatively heavier adrenal glands, and the differences are significant in two of the age classes, but in contrast to the duiker young bushbuck of both sexes have relatively very large adrenals, the highest adrenal index of 37,09 being recorded in a one month old female (Table 4.9 and Figs. 4.27 and 4.28). Thus for a study of possible adrenocortical hypertrophy in this species using the adrenal index, prepubertal animals (under 12 months of age) should be eliminated from the analysis. As in the duiker, those female adult bushbuck with a higher adrenal index have histological differences in both the zona fasciculata and zona reticularis.

TABLE 4.8 Growth in combined adrenal mass with age in male and female bushbuck.

Age (months)	Sex	n	Mean combined adrenal mass (g) ± S.E.	t value and level of significance
1 - 7	M F	4 5	1,662 ± 0,223 1,800 ± 0,070	0,650 n.s.
10 - 19	M F	4 7	2,842 ± 0,413 2,637 ± 0,270	0,434 n.s.
21 - 26	M F	4 4	3,780 ± 0,364 1,920 ± 0,191	4,513 p<0,01
48	M F	7 5	3,528 ± 0,399 2,632 ± 0,110	1,838 n.s.
72	M F	10 17	4,396 ± 0,203 3,564 ± 0,172	3,028 p<0,01
96	M F	21 16	5,422 ± 0,270 3,520 ± 0,217	5,196 p<0,001
132-156	M F	12 11	5,440 ± 0,408 3,551 ± 0,188	4,084 p<0,001

There was no correlation between adrenal weight and cortex/medulla ratio, and even if adrenal weight was corrected for body size through the use of the adrenal index, and prepubertal animals (under 12 months of age) eliminated from the analysis, there was still no correlation, (Figs. 4.29 and 4.30) unlike the duiker.

There was no correlation between adrenal index and KFI in the bushbuck (Figs. 4.31 and 4.32), nor was there any correlation between adrenal index and % DM of marrow samples.

TABLE 4.9 Variation in adrenal index with age in male and female bushbuck.

Age (months)	Sex	n	Adrenal Index ± S.E.	t value and level of significance
1 - 7	M	4	21,860 ± 7,181	0,649
	F	5	17,702 ± 4,919	n.s.
10 - 19	M	4	11,405 ± 1,889	0,562
	F	7	13,101 ± 1,988	n.s.
21 - 26	M	3	11,301 ± 1,937	2,197
	F	4	7,320 ± 0,684	n.s.
48	M	6	7,361 ± 0,261	2,626
	F	5	8,592 ± 0,408	p<0,05
72	M	10	7,630 ± 0,489	3,469
	F	15	10,776 ± 0,661	p<0,01
96	M	20	8,754 ± 0,536	1,538
	F	16	10,020 ± 0,630	n.s.
132-156	M	12	9,866 ± 1,038	0,098
	F	11	9,746 ± 0,595	n.s.

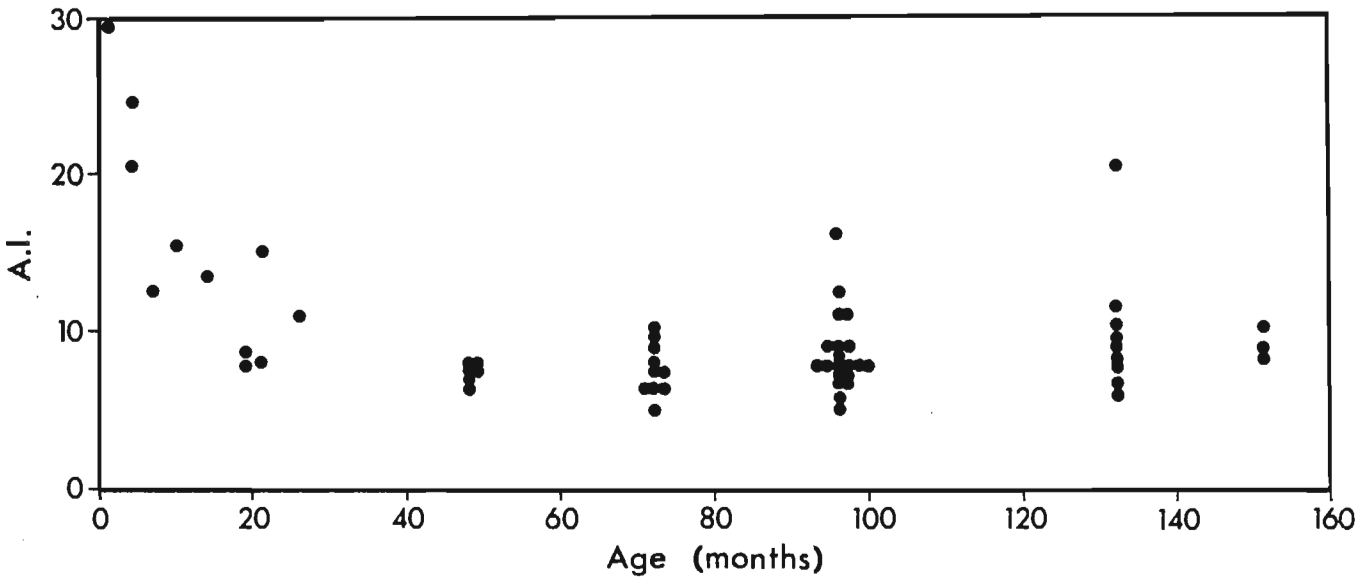


FIGURE 4.27 Growth in relative adrenal mass (adrenal index) of male bushbuck with age.

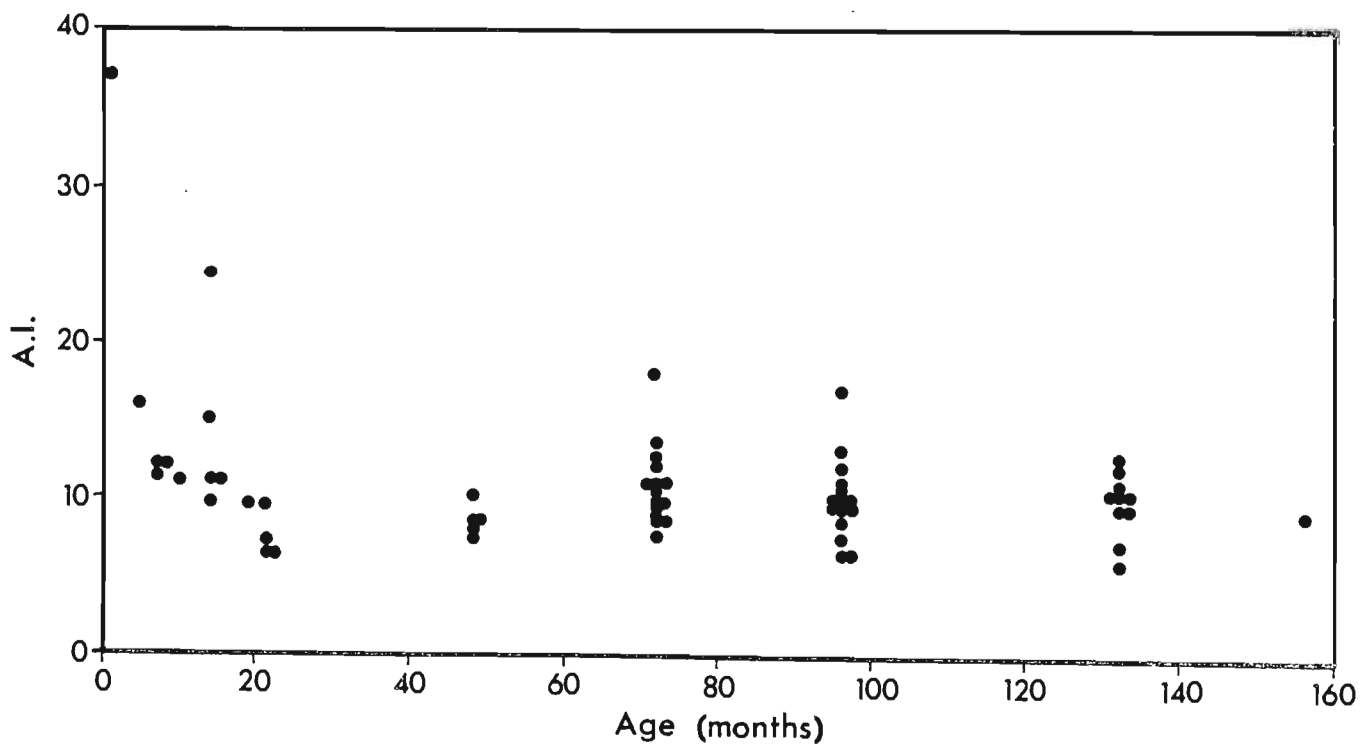


FIGURE 4.28 Growth in relative adrenal mass (adrenal index) of female bushbuck with age.

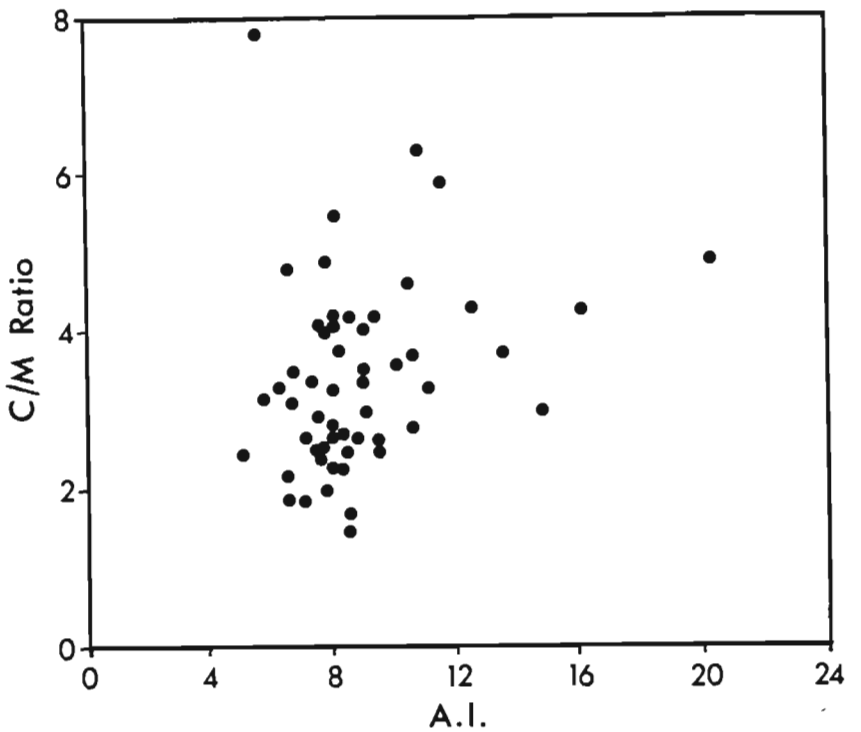


FIGURE 4.29 The relationship between cortex/medulla ratio and adrenal index in male bushbuck.

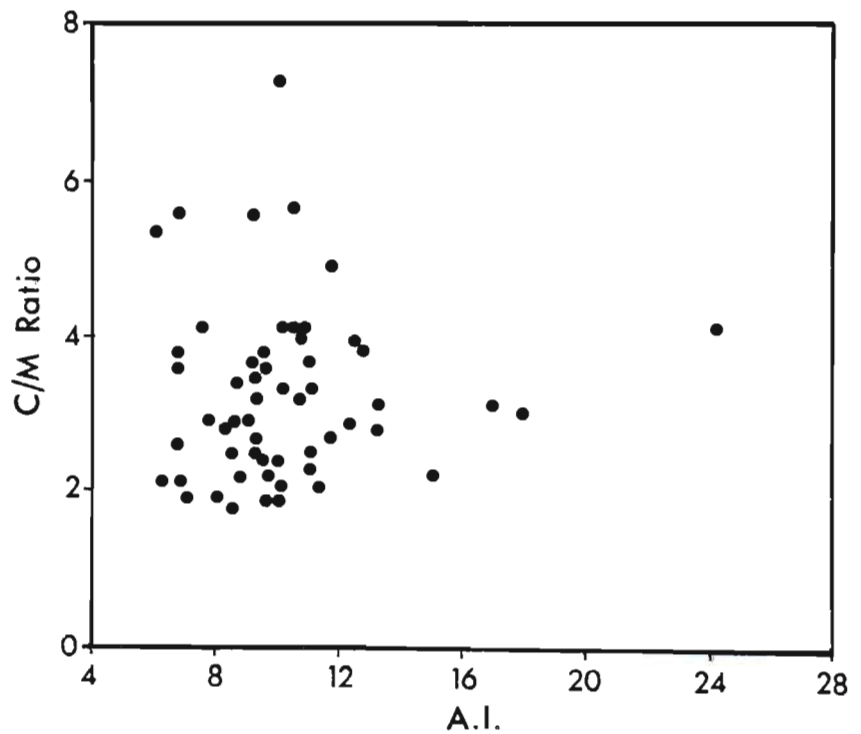


FIGURE 4.30 The relationship between cortex/medulla ratio and adrenal index in female bushbuck.

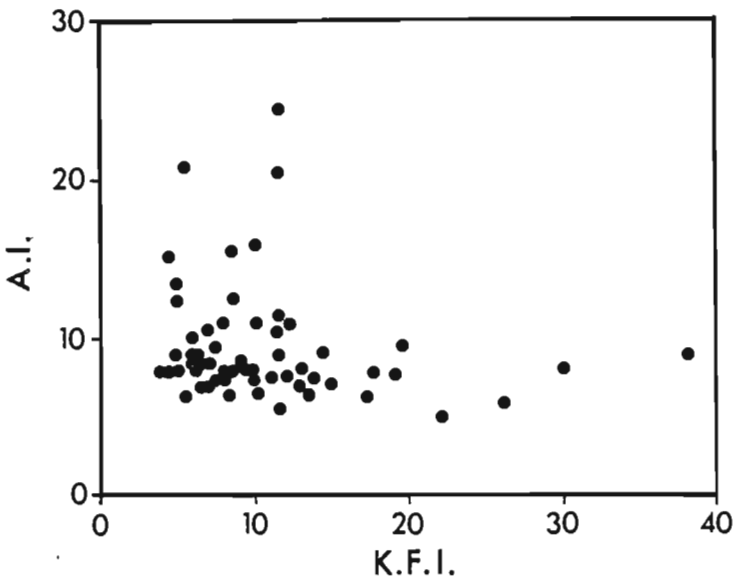


FIGURE 4.31 The relationship between KFI and adrenal index in male bushbuck.

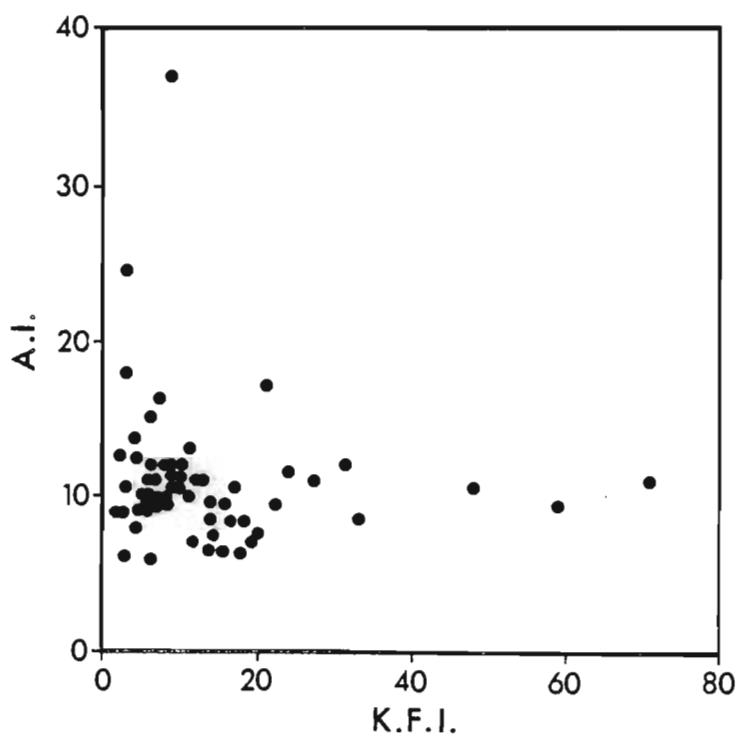


FIGURE 4.32 The relationship between KFI and adrenal index in female bushbuck.

4.3.7 Mortality in Bushbuck

4.3.7.1 Cause of death

Causes of mortality were identified using the criteria detailed in section 4.2 and are detailed for the 31 male and 23 female bushbuck carcasses found during the course of this study in Fig. 4.33. Most of the males (65%) and females (62%) died from natural causes, the major factor being starvation and/or exposure which accounted for 90% and 79% of all natural deaths respectively. None of the males had died from predation or from wounds inflicted by intraspecific fighting, and there were no external injuries on the two adult males that had drowned. Both males and females were susceptible to poaching (snares and dogs) and were killed in road accidents, and similar proportions died from unknown causes (Fig. 4.33). Included in this last category was one male whose carcass was detected, by radio tracking, under a pile of brush and leaves. This animal had probably been killed by poachers but was not utilized, possibly for superstitious reasons. A year later, an isolated but intact radio collar from another male was found in the same area,

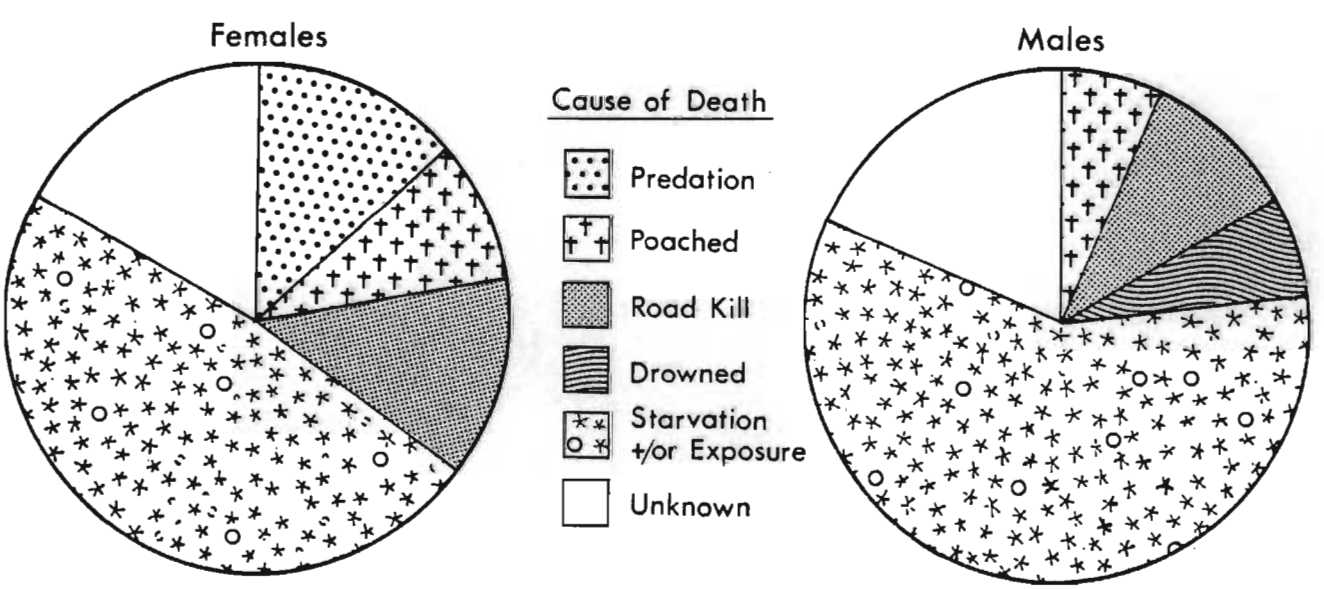


FIGURE 4.33 Cause of death of 23 female and 31 male bushbuck found at Weza during the period September 1980 to October 1984.

and had clearly been removed from the animal since the washers spaced between the nuts and bolts (which were used to fasten the collar) were missing. After an intensive search, this animal (identified by the metal ear tag) was found approximately 300m from the collar, and all of the limbs had been severed and removed from the carcass. Whether the animal had been killed or was found dead and had been butchered is not known. Similarly, the fate of an adult marked female could not be determined since only the radio collar (which had been neatly cut from the animal with a knife) was traced, by telemetry, to the bottom of a stream.

4.3.7.2 Age structure of natural mortalities

The age structure of male and female bushbuck that died from natural causes is shown in Fig. 4.34, which illustrates that 80% of the 20 males and 71% of the 14 females were adults. Most of the males discovered were between 96 and 132 months old, while the majority of females found were slightly younger at 72 to 96 months. Infants (under six months of age) comprised 10% and 7% of all male and female mortalities respectively.

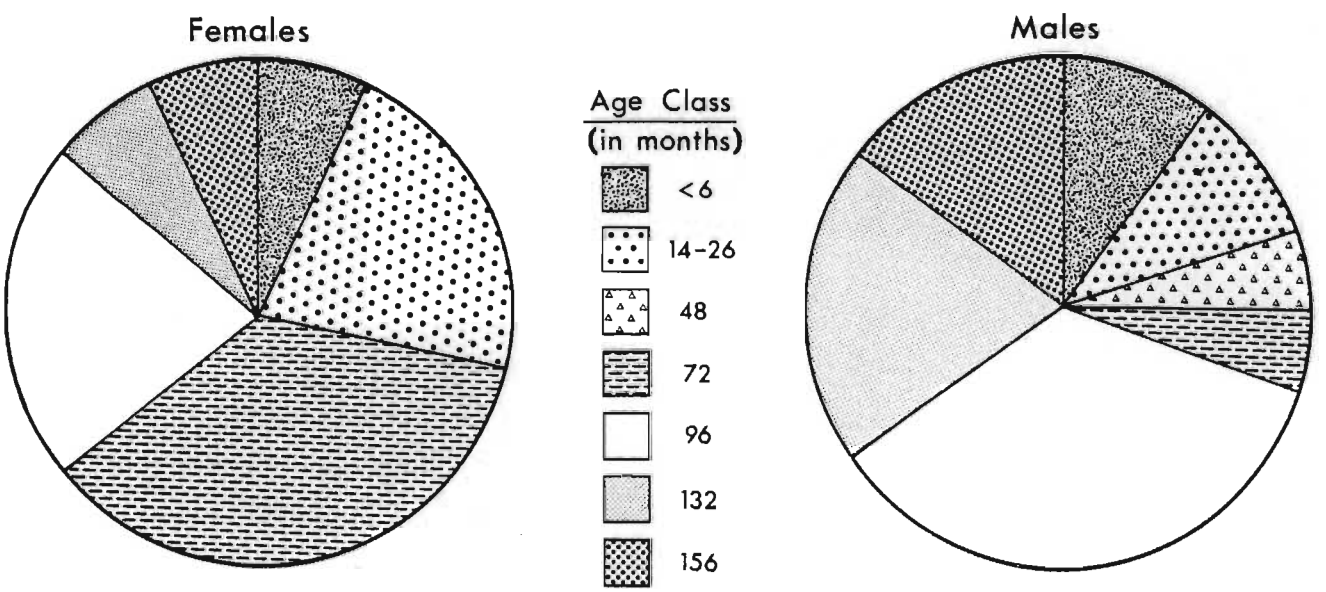


FIGURE 4.34 Age structure of female and male bushbuck that died from natural causes.

4.3.7.3 Temporal distribution of natural mortalities

With the exception of one male that drowned during February, all other natural mortalities that could be accurately dated occurred during the period from April to November, with the majority (65%) occurring in August and September (Fig. 4.35). The two females that died in October were both killed by lynx, while the animal found in November was a one month old male that was considered to have died from starvation, possibly as a result of desertion.

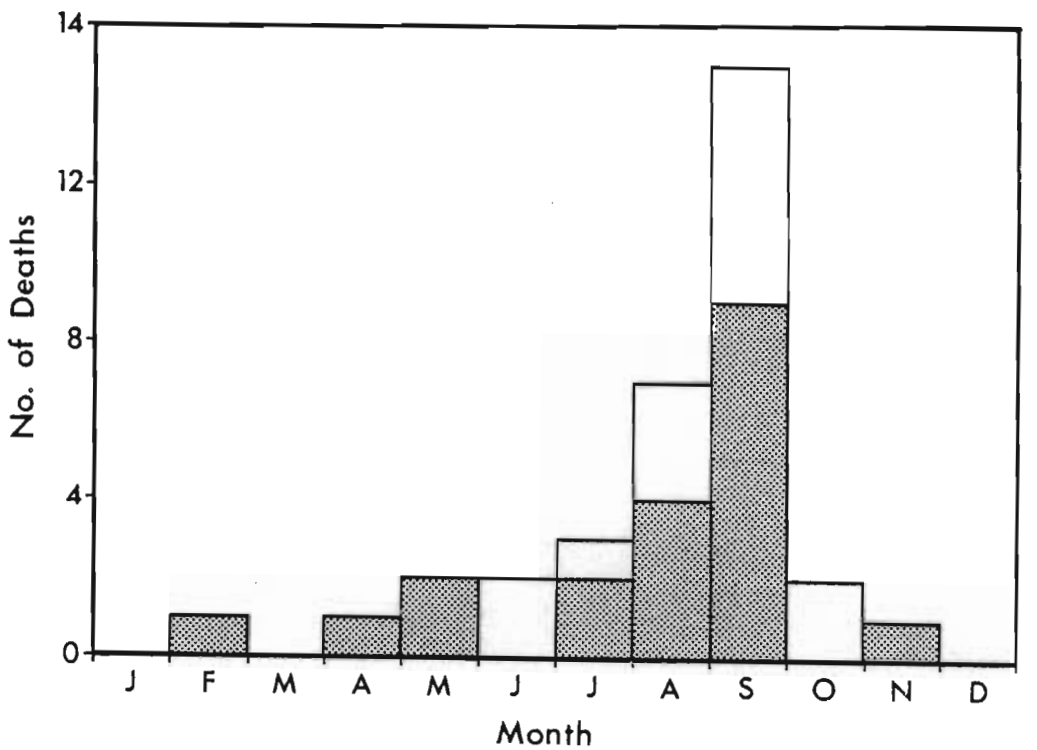


FIGURE 4.35 Monthly distribution of bushbuck deaths from natural causes at Weza (shaded portion represents males).

Shortly after this study commenced seven fresh bushbuck carcasses (three adult males, three adult females and one male infant) were found during a three day period in September. These animals died during and immediately after a period of unusually high rainfall followed by a sudden drop in temperature; these climatic details are illustrated in Fig. 4.36. Two additional bushbuck (one adult male and one subadult female) were found alive during the same time but these were in such a severe state of inanition that they were

unable to rise and were consequently shot. With the exception of the male infant, all of these animals had severely depleted fat reserves and it is highly probable that they succumbed to the synergistic effects of rain and cold at this time. Although similar conditions were experienced at Weza during June and August 1984 (when snow remained on the adjacent mountains for 10 days), no other deaths directly attributable to exposure were recorded.

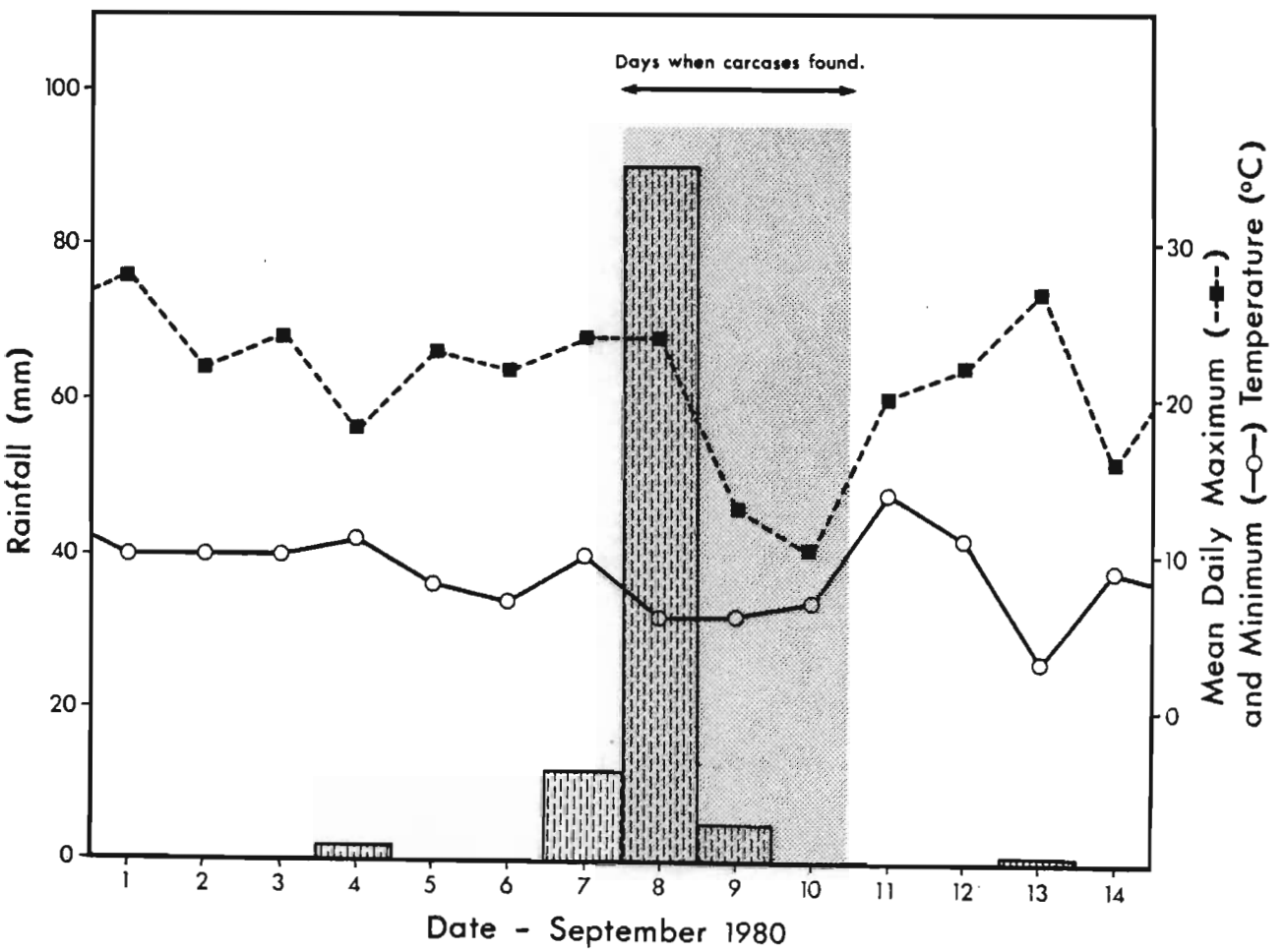


FIGURE 4.36 Daily rainfall and temperature ranges recorded at Weza during the first two weeks in September 1980.

4.3.7.4 Natural mortalities and fat reserves

Condition indices were recorded from relatively fresh carcasses considered to be not more than three or four days old, and hence before putrefaction set in. All adult males

that died from starvation and/or exposure had KFI and % DM values of less than 30 (including the first 132 month old male collected in September that was shot, for reasons given above), while a 4,5 month old male that died in September 1980 (see above) and one of the males that drowned were in relatively good condition (Table 4.10). Two additional males that died from unknown causes have been included in Table 4.10 for comparative purposes, and both had % DM values in excess of 90%.

TABLE 4.10 Month of death, age, and fat reserves of male bushbuck dying from natural and unknown causes.

Age (mths)	Cause of death	Month	KFI	% DM of:		
				Hum.	Rad.	Met.
1	Starvation/exposure	Nov	N/A	20,0	22,5	26,5
4,5	Starvation/exposure	Sep	11,6	40,4	70,0	52,9
14	Starvation/exposure	Jul	4,8	N/A	N/A	N/A
21	Starvation/exposure	Aug	4,5	N/A	N/A	N/A
48	Unknown	May	6,6	N/A	86,7	91,8
72	Starvation/exposure	Sep	6,1	17,7	15,6	20,5
96	Starvation/exposure	Sep	7,9	23,9	21,8	24,9
96	Unknown	Apr	13,2	51,1	93,9	77,3
96	Starvation/exposure	Jul	6,4	18,4	9,6	6,7
96	Drowned	Feb	14,9	31,4	83,9	86,4
132	Starvation/exposure	Sep	11,3	15,7	7,7	13,0
132	Starvation/exposure	Sep	14,4	20,5	10,1	13,1
132	Starvation/exposure	Sep	11,7	18,6	7,4	4,5
156	Starvation/exposure	Aug	3,4	24,2	12,8	11,4
156	Starvation/exposure	May	6,2	18,5	8,7	6,7

N/A - indicates material not available

Without exception, females dying from starvation and/or exposure had condition indices similar to those of adult males that died from the same cause (Table 4.11). The 14 month old female collected in September was shot since she was too weak to move during the wet and cold spell in

September 1980; her KFI and % DM values were all below a value of 15. The condition indices of one female killed by a lynx, and one that died of unknown causes indicate that both of these animals had reasonable fat reserves at their time of death.

TABLE 4.11 Month of death, age, and fat reserves of female bushbuck dying from natural and unknown causes.

Age (mths)	Cause of death	Month	KFI	% DM of:		
				Hum.	Rad.	Met.
1	Starvation/exposure	Aug	8,7	N/A	N/A	N/A
14	Starvation/exposure	Jun	6,4	N/A	N/A	N/A
14	Starvation/exposure	Sep	3,2	12,9	6,4	4,5
72	Starvation/exposure	Jun	11,9	20,9	12,9	7,1
72	Unknown	Sep	10,1	40,7	94,4	95,4
72	Predation (lynx)	Oct	7,2	44,7	80,0	97,6
72	Starvation/exposure	Aug	7,5	N/A	N/A	N/A
96	Starvation/exposure	Sep	11,2	26,9	12,3	9,1
96	Starvation/exposure	Sep	14,9	24,6	8,0	12,6
96	Starvation/exposure	Oct	N/A	20,9	12,2	10,7
96	Starvation/exposure	Sep	16,3	N/A	6,8	8,4
96	Starvation/exposure	Jul	5,1	22,5	14,3	11,9

N/A - indicates material not available

4.3.7.5 Mortality rates

Because of the unequal intervals of time separating each age class, mortality rates could not be determined by conventional life table data. Instead, mortality rates were determined from the proportions of marked animals (for which the totals were known) that died each year. Most other biologists that have adopted a similar approach have monitored mortality only when a sufficient number of subjects have been marked (e.g. Cook et al. 1971; Beale and Smith 1973; Carroll and Brown 1977; Hamlin et al. 1984), but in this study new animals were marked each year from 1981 to 1984. The primary aim of marking additional animals was to

gain more information concerning movements, social organisation and habitat utilization and selection. Consequently, unmarked animals were captured and fitted with radio collars whenever transmitters became available (transmitters were recovered from dead animals or removed from recaptured bushbuck either because they were faulty or because they were approaching their predicted field life; these were checked and invariably fitted with new batteries before being placed on another animal). These additions to the marked population tended to compound problems of estimating mortality rates, particularly since capture operations were most successful at the time when the majority of natural mortalities occurred, i.e. during late autumn, winter and early spring. Furthermore, the mortalities detected in this study are undoubtedly conservative estimates, since it was impractical to equip infants with the rather large transmitter packages used in this study (see Appendix D); all of the animals marked at Weza were older than six months, and only two of the 74 marked bushbuck were less than 12 months old. However, numerous other population studies of ungulates have demonstrated that mortality rates are usually much higher among infants and juveniles than for subadults and adults (Caughley 1966, 1976; Cook et al. 1971; Parker 1972; Mitchell et al. 1977; Hauge and Keith 1981; Ozoga and Verme 1982; Barrett 1982) and consequently the following rates for bushbuck and duiker must be considered as minimum values.

Bushbuck were most intensively monitored in ISA1, where 57 animals were marked during the course of this study. Insufficient numbers of marked animals precluded the determination of mortality rates in 1980 and 1981, but 27 animals had been marked by December 1982. During this year three animals died of unnatural causes, while four natural mortalities (16,7% - i.e. 4/24) were recorded. Thus there were 20 marked animals in ISA1 at the beginning of 1983, and a further 27 animals were marked during the year. Four of these 47 bushbuck died as a result of poaching or road accidents, while 13 bushbuck (30,2%) died of natural causes. These natural mortalities (seven males and six females) were

confined to the period from April to September and represent a mortality rate of 33,3% at this time in an area considered to be prime habitat (see Chapter Seven) which supported a relatively high density of bushbuck (see Chapter Nine). Three additional animals were marked in 1984 and none of these or the 30 animals that survived through 1983 had died of natural causes when field work was terminated in October 1984, although at this time the marked population was reduced to 31 bushbuck as one animal was snared and another had to be destroyed as a result of injury caused during capture.

The temporal distribution of marked bushbuck deaths could not be determined with the same degree of accuracy in other parts of Weza State Forest. Nevertheless, 29 (39,2%) of the 74 marked bushbuck were known to have died (and their collars recovered) during the period from October 1981 to October 1984. Other marked animals may also have died in these three years; nine bushbuck (12,2% of the total marked) were captured and never seen subsequent to their release while seven animals (9,5%) were not observed and could not be radio tracked during the last year of study.

4.3.8 Mortality in Duiker

4.3.8.1 Cause of death

A total of 22 male and eight female duiker were known to have died during the study. A high proportion of both sexes died from unknown causes (Fig. 4.37) while only four of the male and one of the female deaths were natural (starvation, exposure or predation). One female infant died form severe burns caused when forestry staff were burning firebreaks, and four males were each killed by poachers and by road accidents.

4.3.8.2 Age structure of mortalities

Of the natural mortalities, the three males that were killed by lynx were 7 months, 27 months and 180 months old,

and the male and female duiker that died from starvation were 3 months and 4,5 months old respectively. Overall, although there were no significant differences in age-specific mortality rates, 45% of the male and 50% of the female deaths (irrespective of cause) were under 24 months of age.

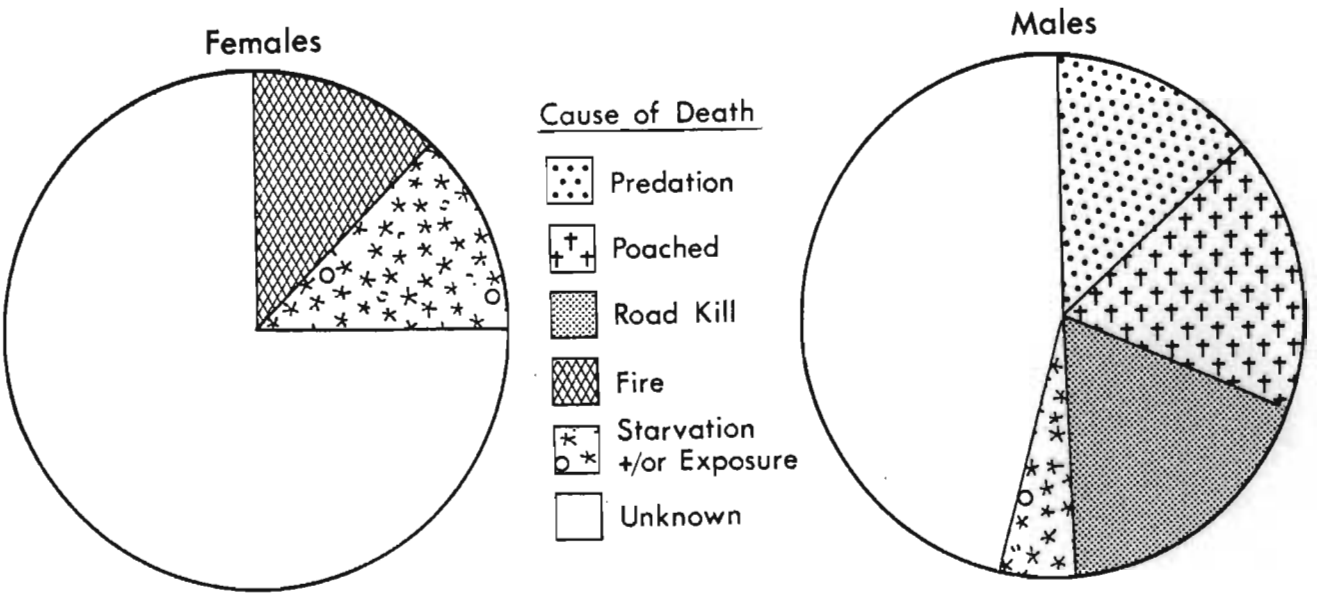


FIGURE 4.37 Cause of death of 8 female and 22 male duiker found at Weza during the period September 1980 to October 1984.

4.3.8.3 Temporal distribution and fat reserves of natural mortalities

The two duiker deaths caused from starvation and/or exposure both occurred during the cold, wet period in September 1980 described earlier in Section 4.3.6.3. The male infant had a KFI of 4,9 and the female had an even lower value of 2,1, while bone marrow samples were not collected in view of the ages of theses animals. The three males killed by lynx were taken in February, August and September, and although KFI (8,1) could be recorded only from the February kill, all three duiker were considered to be in reasonable to good condition, with DM values from the radius and/or metacarpus in excess of 90% in each individual.

4.3.8.4 Mortality rates

Mortality rates were determined in a similar manner to that used for bushbuck, but estimates were based on fewer known individuals, most of which were marked with visual rather than radio collars (see Appendix D). Despite these limitations, at least 15 (39,5%) of the 38 duiker that were marked died during the study period. Mortality rates could not be determined on a seasonal basis because in several instances (three males and two females) the collar but not the carcass was found. (Retrieved collars were included in the mortality data however as all were found intact and showed some degree of wear, yet when fitted all were checked to ensure that each could not slip over the animal's head). Furthermore, cause of death could rarely be ascertained (see above). Nevertheless, a total of 28 animals were marked in 1981, of which two (7,1%) died. A further ten duiker were captured and marked in 1982, when 12 carcasses and/or collars (33,3% of the total marked population minus losses in 1981) were recovered. The number of marked animals therefore declined to 24 at the beginning of 1983, when capture exercises for this species were abandoned, and one death was known to have occurred during the year. One mortality was recorded in 1984 and thus a maximum of 22 marked animals were still alive at the end of field work. However, if the numbers of duiker not seen since capture (one animal) and not seen during the last year of field work (ten animals) are added to the known deaths, these suggest that 26 (68,4%) of the marked duiker may have died during the course of this study.

4.4 DISCUSSION

4.4.1 Mass in Relation to Fat Content of Bone Marrow

In spite of the poor relationship between % fat content and % DM of both radius and metacarpus marrow, these % DM values showed a remarkably similar trend when compared with seasonal fluctuations and age-related changes in KFI and % DM

values from the humerus. The reasons why such a relationship should progressively deteriorate in the intermediate and distal bones are not obvious, and have not been documented previously. Weighing errors magnified by inadequate volumes of marrow from the smaller bones are unlikely to be responsible, since the relationship deteriorated in the distal bones of both species, yet bushbuck limbs are considerably larger than those of duiker. In addition, similar results were obtained when samples were processed in two other laboratories. Brooks et al. (1977) noted a difference in the relationship between % fat content and % DM values of impala marrow when comparing their results to those of Hanks et al. (1976), and suggested that the discrepancy was due to deviations in extraction time. Since all samples from Weza were processed in a Soxhlet apparatus for a minimum of eight hours, it is difficult to envisage how the anomalous results obtained in this study could be due to extraction time, unless the humerus, radius and metacarpus of both bushbuck and duiker contain different types of fat with varying levels of solubility, in much the same way that marrow from different bones exhibits different melting points (Irving 1966 cited in Peterson et al. 1982). Whatever the cause, the relationship between % fat content and % DM values of bushbuck and duiker marrow warrants further attention.

Although Caulton and Bursell (1977) have questioned the accuracy of results obtained using fat-water relationships to estimate bone marrow fat content, numerous other authors (reviewed in section 4.1.1.2) have demonstrated a positive and highly significant relationship between fat content and dry mass values. However, these studies have almost invariably been concerned with marrow from the proximal limb bone, usually the femur, the dry mass of which also provides a good quantitative estimate of its fat content in bushbuck and duiker. Since this study has shown that the relationship between fat content and dry mass of marrow is less reliable for the medial and distal bones, such relationships should also be examined in other species. At present, there is a tendency to extrapolate femur marrow predictive equations (e.g. Sinclair and Duncan 1972; Brooks et al. 1977; Hanks

1981) to medial and distal bone marrow samples (e.g. Brooks 1978; Fong 1981; Reich 1981; Melton and Melton 1982a), or to marrow samples from other unrelated species (Schmidt 1984b). Assuming that the results of this study are not peculiar to bushbuck and duiker at Weza, such extrapolations may well result in erroneous assessments of stored fat reserves.

4.4.2 Fat Reserves of the Bushbuck and Duiker

This study has demonstrated that bone marrow fat in bushbuck and duiker is mobilized after perinephric fat and is therefore a better measure of physiological condition once KFI values have fallen below a value of about 20. Further, because dry mass values of the humerus rarely fall below 20% (when virtually all of the marrow fat has been utilized) or exceed 80% at Weza, the humerus marrow should be analysed in conjunction with one or preferably both of the other long limb bones for more accurate assessments of condition in these two species. Animals in chronically poor condition (i.e. exhibiting a metacarpus DM value of less than 50%) would provide an exception to this guide however; the sequential pattern of fat mobilization within the forelimb indicates that little would be gained by examinations of the proximal and medial bone marrows in such instances.

In contrast to duiker, female bushbuck at Weza have significantly greater mean annual stored fat reserves than males. Females attaining higher levels of physiological condition than males have also been reported in the congeneric nyala (Anderson 1978) and several temperate ungulates (e.g. Flook 1970; Bear 1971; Mitchell et al. 1977). While a decline in the condition of males may be attributable to the rut in many species (e.g. Anderson 1965; Flook 1970; Dauphine 1977; Brooks 1978; Knowlton et al. 1979; Dunham and Murray 1982; Clutton-Brock and Albon 1983), the fat reserves of male bushbuck are not influenced by any seasonal reproductive cycle (see Chapter Five). Consequently, other factors must be responsible for these sex differences in physiological condition, the most plausible of

which concerns body size.

Since adult male bushbuck are almost twice the size of adult females, their food requirements for growth and maintenance are obviously greater. Using metabolic mass values, i.e. body mass to the power three-quarters (e.g. Hoar 1966; Buechner and Golley 1967; Alexander 1971; Robbins and Moen 1975; Smith et al. 1975; Western 1979; Bryant et al. 1980; Robbins et al. 1981; Owen-Smith 1982; Owen-Smith and Novellie 1982; Clutton-Brock and Harvey 1983; Coe 1983; McNab 1983; Wheaton and Brown 1983; Hoppe 1984a), several authors have shown that the basal metabolic rate of many ungulates approximates 70 Kcal per day per kg of metabolic mass (Kleiber 1961; Blaxter 1962; Silver et al. 1969; Hardy 1972; Krebs 1972; Moen 1973; Coe 1983). Applying this "interspecific mean basal metabolic rate" (Short and Golley 1968; Moen 1973; Stanley Price 1978; Regelin 1979; Kautz et al. 1982) to bushbuck, males that have attained asymptotic mass would require approximately 1500 Kcal per day, while adult females would require 1000 Kcal per day. These differences in energy requirements may therefore explain why females were generally in better condition than males, particularly at times when food quality and quantity was limited. The almost identical energy requirements of male and female duiker (513 Kcal per day and 573 Kcal per day respectively, determined in the same manner as for bushbuck) which did not exhibit significant intersexual differences in stored fat reserves, corroborate this conclusion.

Obviously these are minimal values since they reflect the energy requirements of fasting individuals in a thermoneutral environment. Maintenance or activity requirements of African ungulates have rarely been determined (notable exceptions include Rogerson (1968), Sinclair (1977) and Stanley Price (1978)), but the additional energetic costs of thermoregulation, locomotion, tissue maintenance and production, gestation and lactation have been assessed in a number of temperate species. For example, Brody (1945) estimated that the average metabolic costs of maintenance (i.e. excluding growth or reproduction) were twice the basal

metabolic requirements, which Wallmo et al. (1977) confirmed for mule deer, while Blaxter (1962) generalised that maintenance needs of a ruminant were 1,36 times its fasting requirement, and Owen-Smith and Novellie (1982) suggested that maintenance requirements for kudu equalled 1,6 times the basal metabolic rate. Gates and Hudson (1979) demonstrated that white-tailed deer maintained in thermoneutral conditions increased their energy expenditure by 30% and 82% when their activities changed from lying to standing and moving respectively, and Kautz et al. (1982) estimated that active mule deer would require 1,9 - 2,9 times the energy needed for basal metabolism. Estimates of total energy expenditure by large herbivores have been as high as three times basal metabolic rate (Lamprey 1964; Gessaman 1973 cited in Litvaitis and Mautz 1980; Eltringham 1974) but are usually considered to be lower, between 1,23 to 1,98 times basal metabolic rate, depending on how much time is spent in various activities (Moen 1973; Wallmo et al. 1977; Regelin 1979; Coe 1983). Numerous other examples of the energetic requirements for different ungulate species can be found in Ullrey et al. (1969), Thompson et al. (1973), Mitchell et al. (1977), Mautz (1978), Baker et al. (1979), Parker et al. (1984) and do not need to be detailed here; the above examples clearly demonstrate that the additional metabolic costs of maintenance would amplify intersexual differences in the energy requirements of bushbuck but not of duiker.

Numerous other wildlife studies have demonstrated that aspects of reproduction are important factors affecting, and affected by, body mass and condition in adult ungulates (e.g. Verme 1965, 1969; Sadleir 1969a, 1969b; Lincoln et al. 1970; Guinness et al. 1971; Lincoln and Guinness 1973; Mitchell and Lincoln 1973; Mitchell and Brown 1974; Thorne et al. 1976; Guinness et al. 1978a; Ozoga and Verme 1982; Albon et al. 1983), and Mitchell (1973) regarded the mature non-pregnant, non-lactating female red deer as a symptom of nutritional stress. Although there is no evidence that fertility in adult bushbuck and duiker at Weza is influenced by physiological condition (see Chapter Five), the fat reserves of both species varied significantly with reproductive

status. Pregnant but not lactating females had the most extensive fate deposits, while pregnant and lactating females were invariably in the poorest condition. These differences are undoubtedly due in part to the varying energetic demands imposed by gestation and lactation. Both energy and protein requirements of female ungulates are typically slight in the first two-thirds of gestation but increase logarithmically during the last third (Verme 1965; Moen 1973). Costs of lactation are higher than those of pregnancy (Sadleir 1969a, 1969b; Hanwell and Peaker 1977; Clutton-Brock et al. 1982a) and often peak during the fourth to sixth week after parturition, at which time they may reach 2,3 times the basal metabolic rate (Moen 1973, 1978), or more than double normal maintenance requirements (Sinclair 1977). To compensate for this, red deer hinds offered ad libitum supplies of food will eat up to 2,6 times the maintenance requirements of non-breeding animals of similar mass (Arman et al. 1974) and similar increases have been recorded in other ungulate species (e.g. Corbett 1964 cited in Clutton-Brock et al. 1982b; Moen 1973). Presumably, where food quality or quantity is limiting, females obtain these additional requirements by catabolizing stored fat and protein reserves. The depleted fat reserves of lactating and pregnant females of both species (which in bushbuck are comparable to the fat reserves of adult males) therefore strongly suggest that both bushbuck and duiker are receiving inadequate nutrition for at least part of the year at Weza. Perinephric fat reserves of both adult bushbuck and duiker females (Figs. 4.38 and 4.39 respectively), indicate that late winter and spring is the most critical time, but unlike pregnant females, lactating bushbuck and duiker are rarely able to store extensive fat reserves at any time of the year.

The fact that juvenile and subadult bushbuck had significantly lower fat reserves than adults is in accord with the studies of other species by Dauphine (1976), Franzmann and Arneson (1976), Hanks et al. (1976), Fong (1981), and Dunham and Murray (1982), and is no doubt largely due to the higher energetic demands of growth in young animals. However, differences in the fat reserves of

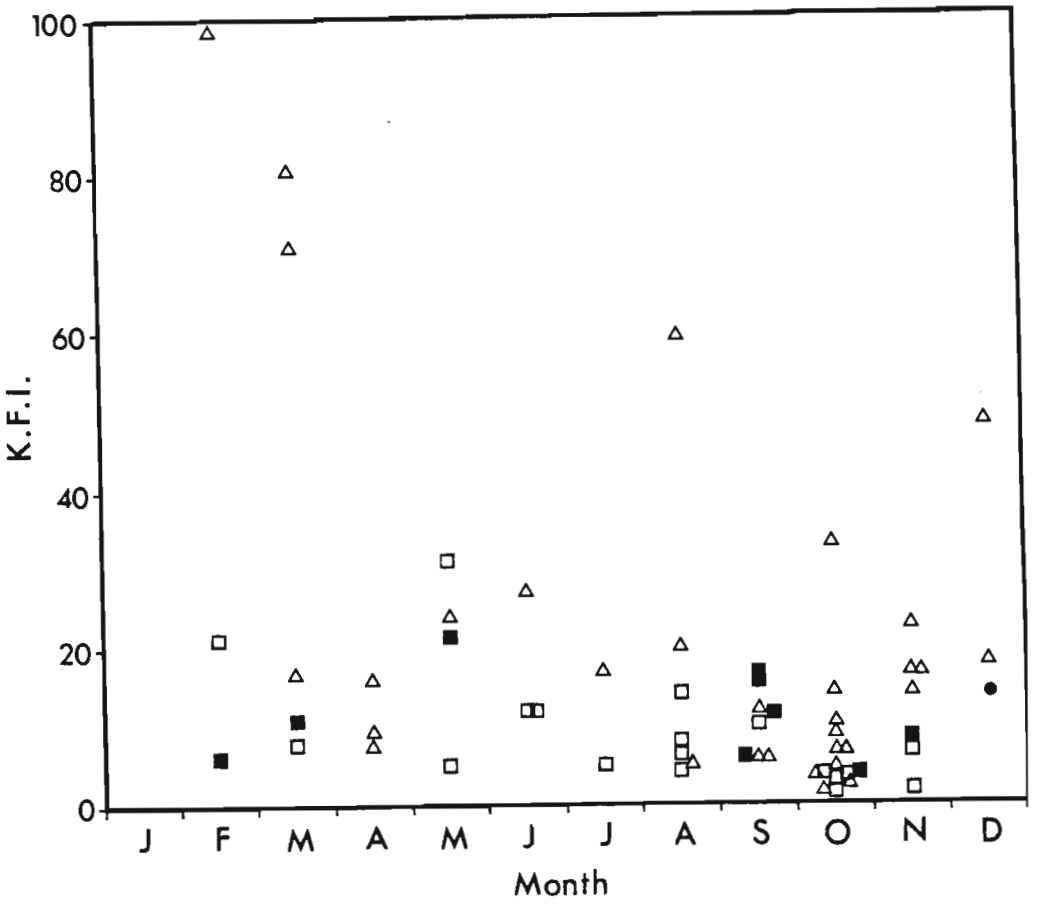


FIGURE 4.38 Monthly variation in KFI values of adult female bushbuck in relation to reproductive status (open circle - pregnant; closed square - lactating; open square - pregnant and lactating; closed circle - not pregnant, not lactating).

subadult and adult duiker were much less pronounced. The results obtained from examinations of the fat reserves of this species therefore do not support Hanks' (1981) comment that very little body fat is deposited in younger animals, regardless of condition. The 2,5 month old reindeer illustrated in Plate 2(a) also refutes Hanks' (1981) statement, while recent studies (Verme and Ozoga 1980a,b) suggest that lipogenesis in white-tailed deer fawns is an obligatory physiological event in autumn, and "proceeds despite undernutrition until a serious negative energy balance occurs". In older female deer, maximum condition appears to be attained approximately two years earlier than maximum body size (Mitchell et al. 1977). These findings therefore demonstrate that extensive fat reserves may in fact be deposited long before growth is completed, and

consequently material from younger animals should not necessarily be immediately discarded in condition analyses.

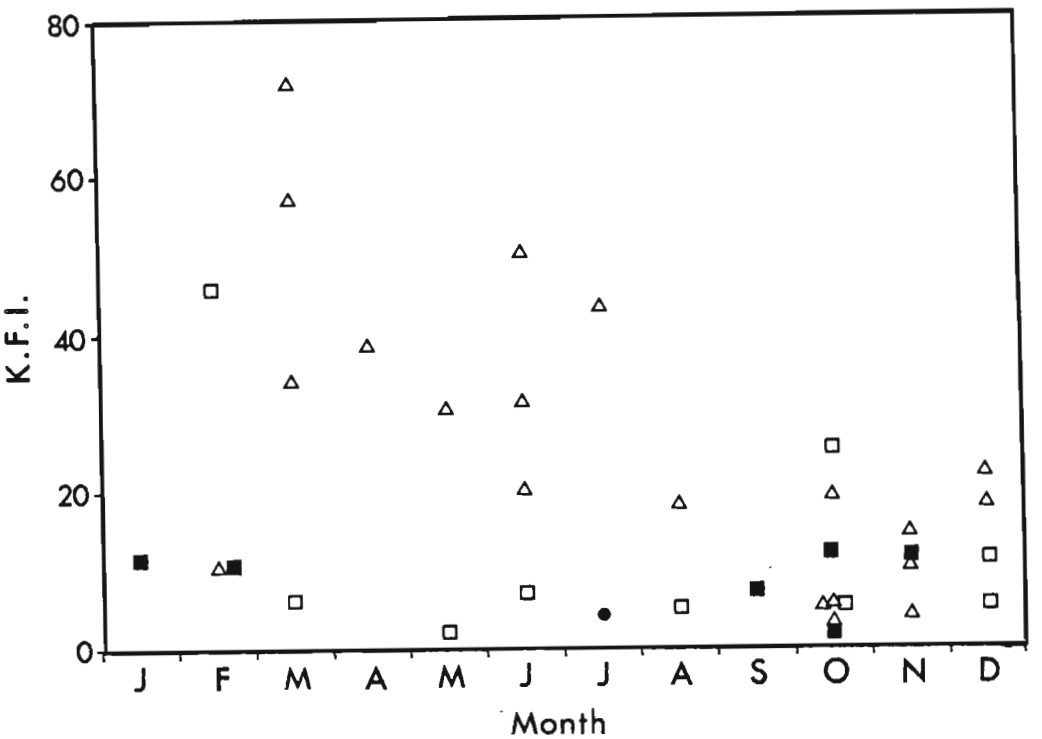


FIGURE 4.39 Monthly variation in KFI values of adult female duiker (20 months +) in relation to reproductive status (open triangle - pregnant; closed square - lactating; open square - pregnant and lactating; closed circle - not pregnant, not lactating).

Reasons for the age-related differences between the fat reserves of bushbuck and duiker are not known. These may partly be due to the much more rapid growth rate of the latter species (see Chapter Three), but may also be influenced by differences in diet selection and quality (see Chapter Six), or by the availability of suitable forage, particularly since both male and female duiker are territorial and together with their immature offspring presumably experience less intraspecific competition than bushbuck (see Chapter Eight).

In contrast to duiker, adult male and female bushbuck exhibited pronounced annual cycles of condition. Since KFI

values of both sexes gradually declined from their highest levels in summer and were lowest in spring (Tables B.1 and B.5), these results suggest that the most nutritious food for bushbuck at Weza is available during late spring/early summer, after the onset of the summer rains. Bone marrow fat reserves were also lowest in spring, but unlike KFI's these did not rise substantially in summer, but increased gradually until they reached their highest values in winter (Tables B.2 to B.4 and B.6 to B.8). This suggests that lipogenesis, like mobilization, occurs sequentially and commences around the kidneys before proceeding to the more distal regions of the body. Further, the rapid decline in % DM values from all three long limb bones during the interval between winter and spring (when perinephric fat reserves are also most depleted) infers that this is the most critical time of the year for this species at Weza. Bushbuck surviving this period rapidly gain in condition and by summer have more extensive perinephric fat reserves than at any other time of the year.

Several authors have reported that cervids decline in physiological condition during the winter months even when there is abundant food available, and have concluded that loss in condition is directly attributable to extremely cold weather (e.g. Verme 1962 cited in Verme 1968; Ransom 1967). More recent studies however, have shown that many ungulates from temperate zones reduce their voluntary food intake and metabolism during the winter months (e.g. Wood *et al.* 1962; Silver *et al.* 1969; Bandy *et al.* 1970; McEwan and Whitehead 1970; Ozoga and Verme 1970; Thompson *et al.* 1973; Alldredge *et al.* 1974; Kirkpatrick *et al.* 1975; Short 1975; Smith *et al.* 1975; Holler *et al.* 1976b; Wallmo *et al.* 1977; Moen 1978; Knowlton *et al.* 1979; Regelin 1979; Westra and Hudson 1981; Carpenter 1984; Langer 1984) even when high quality food is provided (Drozdz and Osiecki 1973; Blaxter *et al.* 1974 cited in Mitchell *et al.* 1976; Pollock 1974; Mitchell *et al.* 1977; Mautz 1978; Hawley 1981 cited in Barrett 1982; Clutton-Brock *et al.* 1982a). This reduction in food intake is probably triggered by changes in day length (Simpson 1976 cited in Mitchell *et al.* 1976; Kay 1978 cited in Clutton-Brock *et al.* 1978; Moen 1978; Kay and Staines 1981 cited in Clutton-Brock

et al. 1982a; McMillin et al. (1980) cited in Wheaton and Brown 1983), and is most pronounced in those species that exhibit annual cycles of growth and seasonal patterns of reproduction (Regelin 1979). Presumably, this mechanism helps to reduce the energetic costs of feeding in situations where the quality of quantity of food does not allow individuals to cover their daily requirements (Mitchell et al. 1977) although as Clutton-Brock et al. (1982a) point out, it is not clear why such an inflexible system is adaptive. Although Stanley Price (1977, 1978) has reported a similar phenomenon in Coke's hartebeest, which has adapted to a semi-arid environment, it is difficult to envisage how the decline in physiological condition of bushbuck could be due to a lower food intake and reduced metabolic requirements during the winter, particularly since the species selects relatively stable habitats over much of its range (see Chapter One) and breeds throughout the year (see Chapter Five). Further, activity budgets of this species at Weza do not suggest a decline in either foraging or metabolism during winter (see Chapter Eight), while the congeneric nyala and kudu have been shown to be most active at this time of the year (Anderson 1978; Owen-Smith 1979). It is therefore reasonable to assume that the decline in physiological condition of both male and female bushbuck at Weza is directly attributable to inadequate nutrition at Weza during the winter and early spring. The greater fat reserves of bushbuck on adjacent farms, where alternative food resources are available at this time, corroborate this conclusion.

The seasonal fat reserves of duiker differed notably from those of bushbuck. Perinephric fat reserves of both sexes were most extensive during the autumn months, but thereafter declined during the winter and were most depleted in spring. As in bushbuck, duiker % DM values from the marrow of all three limb bones were also lowest in spring, but did not differ significantly from values recorded at all other times of the year. These data suggest that while the duiker's nutritional requirements are not met during late winter and spring, only partial catabolism of stored fat reserves is necessary to correct the net imbalance. Thus

this period appears to be less critical for duiker than for bushbuck.

Smaller amplitudes in the seasonal variation of stored fat reserves of the duiker may be associated with the level of social organisation exhibited by this species (see Chapter Eight). However, an equally plausible explanation for the differences in physiological condition of bushbuck and duiker concerns diet selection. Although small-sized herbivores have lower absolute food requirements than larger species, they have higher metabolic rates per unit of body tissue (Kleiber 1961; Odum 1971; Ricklefs 1973; Coe 1983; McNab 1983) and consequently small antelope would be expected to select food with a relatively high nutritional value (Bell 1971; Clutton-Brock and Harvey 1983). Assuming that throughput rate does not change with body size, Owen-Smith (1982) has calculated that the minimum level of crude protein in the diet required for minimum maintenance would be 5% for a 500 Kg ruminant, 9% for a 50 Kg animal and 16% for a species weighing 5 Kg. Although the nutrient content of forage plants was not analysed in this study, distinct differences were evident in the selection of plant parts and species by bushbuck and duiker (see Chapter Six). Assuming that the nutrient content of the principal food items selected by duiker (fruits and fungi) was greater than the principal food items eaten by bushbuck (mainly browse) then plant phenology would largely account for the discrepancy in the times when each species had most extensive perinephric fat reserves. Non-significant differences between the fat reserves of duiker for plantations and from surrounding farms during the winter, further support the conclusion that this species is on a higher nutritional plane than bushbuck at Weza.

4.4.3 Adrenocortical Hypertrophy

From comparative studies of a large number of mammals (Goertz 1965; Krumrey and Buss 1969; Morris 1973; Vaughan and Keith 1981; Kie *et al.* 1973), the adult female adrenal is

heavier than that of the adult male, and this is due to an enlarged zona reticularis (Bourne 1949). The female adrenal also undergoes changes in the sexual cycle, with cortical hypertrophy at oestrus, and in pregnancy and lactation (Christian 1962; Chitty and Clark 1963; Krumrey and Buss 1969; Plotka et al. 1983). As all the adult females, with the exception of one bushbuck and one duiker, collected in this study were either pregnant and/or lactating, the adrenocortical hypertrophy observed is probably related to reproductive activity, and not to social stress. A preliminary study of those bushbuck and duiker with higher cortex/medulla ratios has revealed histological differences in both the zona fasciculata and zona reticularis. These differences are at present the subject of a more detailed investigation by Allen-Rowlandson et al. (in prep.).

A marked decline in relative adrenal mass at puberty, followed by a pattern of growth in which adult females had relatively heavier adrenal glands has also been described in bushbuck collected in Zimbabwe by Morris (1973). These results are in direct contrast to those obtained for duiker, and may possibly be explained by the fact that young bushbuck at Weza are, relatively speaking, in much poorer condition than adults of either sex. Another intriguing possibility is that adrenocortical hypertrophy occurs in pubertal duiker at a time when they are subjected to social stress caused by eviction from parental territories, and as they move into marginal habitats or seek territories of their own (see Chapter Eight).

Although several authors have attributed an increase in adrenal mass to stress induced by high population densities or inadequate food reserves, these studies have all involved small mammals (e.g. Christian 1955, 1975; Andrews 1968; To and Tamarin 1977; Vaughan and Keith 1981). Hughes and Mall (1958) reported a negative correlation between adrenal mass and perinephric fat in black-tailed deer, but their kidney fat reserves were visually assessed rather than measured quantitatively; Welch (1962) reported that deer collected from a high density, overbrowsed range had higher relative

adrenal mass values when compared to animals from a range in good condition, and similar data and interpretations have been presented for roe deer (Capreolus capreolus) by Wandeler (1966), Bubenik and Bubenik (1967) (both cited in Seal et al. 1983), and Klein and Strandgaard (1972). However, in none of these instances were differences in adrenal mass significant, and numerous other studies, including this one, have shown that age and age-related variables may account for most of the observed variation in adrenal mass (e.g. Hoffman and Robinson 1966; Flook 1970; Anderson et al. 1971; Kie et al. 1983; Seal et al. 1983).

With the elimination of prepubertal animals from the analysis, this preliminary study has shown that in the Weza area the bushbuck collected showed no evidence of adrenocortical hypertrophy, in spite of considerable variation in deposited fat reserves. Since there was also no correlation between adrenal index and KFI or between adrenal index and % DM values of bone marrow in the duiker, it is evident that the adrenal glands of both species are of limited use as a direct or supplementary index of physiological condition. As in this study, Smith (1970), Verme (1979), Attwell (1982a) and Howard (1983) were unable to demonstrate any relationship between adrenal mass and physiological condition (as measured by fat reserves), and it is obvious that controlled experimental work is urgently required before adrenal measurements can be of any practical value in wildlife management (Hanks 1981). In addition, Attwell (1982a) has questioned the use of the adrenal index since total mass measurements may be imprecise (due to blood loss, scale inaccuracies, ingestion of food or water before death etc.). Anderson et al. (1971) have further shown that adult deer can vary in body mass with little change in absolute adrenal mass. Since bushbuck undergo pronounced and significant seasonal changes in total body mass, comparisons of relative adrenal mass could give a misleading impression regarding hypertrophy or hyperplasia in this species. A technique relating adrenal mass to some skeletal parameter (which would not be subjected to seasonal fluctuations and would more accurately reflect physiological age, Klein 1964)

may therefore provide a more sensitive and appropriate measure of adrenocortical hypertrophy.

4.4.4 Mortality

Caughley (1966) concluded that mortality patterns in mammals typically follow a "U" shaped trend with age, i.e. with juvenile and old-age animals having higher mortality rates than those of young or prime adults. Mortality rates of neonates and young ungulates are particularly high because these animals are often more vulnerable to predators (Sadleir 1969a; Spinage 1970; Cook et al. 1971; Beasom 1974; McDiarmid 1974; Miller and Broughton 1974; Carroll and Brown 1977; Leuthold 1977; Wolfe 1977; Kie et al. 1979; Ballard et al. 1981; Hauge and Keith 1981; Carbyn 1983; Barrett 1984; Hamlin et al. 1984). Poor condition through inadequate nutrition may also constitute another principal cause of pre- and post-natal mortality, operating directly or in association with other secondary factors such as exposure, disease, maternal neglect, etc. (Robinette et al. 1957; Mitchell et al. 1971; Roth et al. 1972; Wilson et al. 1974; Arman 1974; Wegge 1975; Mitchell and Staines 1976; Thorne et al. 1976; Verme 1977; Wilson and Hirst 1977; Guinness et al. 1978b; ; Staines 1978; Jeffery 1979; Melton and Melton 1982a; Ozoga and Verme 1982; Ozoga et al. 1982a, 1982b; Sauer and Boyce 1983). Therefore, any detailed discussion concerning mortality rates should incorporate data from the infant and juvenile segments of the population being studied. However, because all of the bushbuck and duiker marked in this study were, for practical reasons at least seven months old, the only direct data concerning juvenile mortality were obtained from the few carcasses found in the field. Consequently, the following discussion is confined to the causes and patterns of mortality in older bushbuck and duiker; indirect methods used to assess neonatal and juvenile mortality rates, and conclusions regarding population performance are more appropriately detailed later in this thesis (see Chapter Ten).

With the exception of data obtained from telemetry, it is highly probable that inconsistencies regarding the notification and/or collection of carcasses found in the field biased subsequent assessments of the causes of mortality. Although the greatest proportion of bushbuck deaths was due to natural causes (Fig. 4.33), this is considered to be an obvious under-estimation, since many carcasses were probably not detected or reported. Conversely, because forest guards are instructed to notify the relevant authorities of any illegal activities encountered within Weza, the incidence of poaching is considered to be grossly over-estimated when compared to the proportions of animals that died from other causes. The proportion of animals that died from road accidents is also likely to be an over-estimate, for similar reasons.

Nevertheless, results from this study demonstrate that starvation/exposure during the winter and early spring is responsible for the majority of adult male and female bushbuck deaths at Weza. Most of these deaths occurred in 1980 and 1983. Reported deaths in 1980 were undoubtedly due to the synergistic effects of low temperatures and high rainfall during September. Mortalities resulting from similar environmental conditions have been reported in the congeneric nyala and kudu (Wilson 1970; Keep 1973; Anderson 1978) and other African ungulates (Ferrar and Kerr 1971; Brooks 1973 cited in Howard 1983), while there are numerous examples of increased mortality in cervids following harsh weather or severe winters (e.g. Mitchell et al. 1971; McDiarmid 1974; Mitchell and Staines 1976; Clutton-Brock and Albon 1982). However, it should be noted that cervid mortalities in winter are often associated with snow accumulation rather than rainfall (e.g. Klein and Olson 1960; Klein 1968; Flook 1970; Wegge 1975; Crete 1976a, 1976b; Dauphine 1976; Barrett 1982; Durbin 1984) which may cause further starvation by restricting movement and reducing foraging efficiency (Mautz 1978; Carpenter 1984).

In contrast to 1980, bushbuck deaths from natural causes in 1983 were not confined to any specific period of the

winter or to sudden changes in climatic conditions, and were therefore probably due to starvation rather than exposure. Malnutrition probably resulted from the drought conditions experienced during the preceding rainfall season, when Weza received only 72% of the average rainfall (see Chapter Two), and bushbuck presumably were unable to deposit extensive fat reserves during summer and autumn. This conclusion is supported by the studies of Lowe (1969), Anderson (1972) cited in Mitchell et al. (1977), and Beddington (1973) cited in Clutton-Brock and Albon (1982) who found good correlations between summer rainfall and natural mortality in red deer the following winter. In addition, Dauphine (1976) considered that the full recovery of all fat deposits in summer was of critical importance to subsequent winter survival of caribou, and similar findings elsewhere have emphasised the importance of research into the nutrition available to ungulates during the summer months (e.g. Bobek 1977a; Mautz 1978; Baker and Hobbs 1982). Above average rainfall during the 1983-1984 season (116%) and the absence of any deaths from natural causes in 1984 strengthen the conclusion that malnutrition is influenced by rainfall during the preceding year, although a reduction in population numbers (as evidenced by the proportion of marked animals that died in 1983), and hence less intra-specific competition, may have contributed to the enhanced survival witnessed in 1984.

Other common causes of natural mortality in ungulates include predation (e.g. Wright 1960; Klein 1965, 1970, 1981; Parker 1972; Miller and Broughton 1974; Wolfe 1977; Connolly 1978), diseases and other pathological disorders (McDiarmid 1974, 1975; Wilson et al. 1974; Mitchell et al. 1977; Wilson and Hirst 1977; Grobler 1978; Melton and Melton 1982a) and injuries resulting from fighting (e.g. Bergerud 1971a; Geist 1971a; Wilkinson and Shank 1976; Clutton-Brock et al. 1979). Of these, only predation by lynx had any influence on the bushbuck population at Weza, and this was confined to females and young (adult males presumably exceeded the maximum prey-handling size of this predator, see Grobler (1981)). A detailed parasitological survey conducted for thirteen months (1982-1984) has revealed that both bushbuck and duiker have

remarkably few ecto- and endo-parasites throughout the year at Weza (M. Keep, pers. comm.), while none of the male bushbuck carcasses examined had injuries that could be attributable to fighting. These results therefore demonstrate that the major natural cause of death in bushbuck is starvation and/or exposure.

Analyses of the sex and age structure of bushbuck dying from natural causes were limited by the low numbers of carcasses that were recovered. Although not statistically significant, the number of males that died from starvation and/or exposure was more than 60% higher than females (Fig. 4.33). Similar male biased mortality has also been reported during die-offs in several other species (e.g. Klein and Olson 1964; Klein 1965, 1969, 1970, 1981; Child 1972; Crowe and Liversidge 1977) and is considered to result from the higher metabolic requirements of males when food becomes limiting and their inadequate fat reserves which are more depleted than females after the rut (Flook 1970; Klein 1970; Grubb 1974a; Dauphine 1976). In this regard it is interesting to note that all of the nine adult female bushbuck that died from starvation/exposure were reproductively active; one was pregnant, three were lactating and five were both pregnant and lactating.

In many temperate ungulates, population density, the nutritional quality of the habitat and climatic factors interact in their effects on populations (e.g. Klein 1965, 1968, 1970, 1981; Verme 1969, 1977; Grubb 1974a; Barrett 1982), and consequently it is often difficult to separate the effects of density from those of weather variation (Clutton-Brock et al. 1982a). Natural mortalities of animals inhabiting adequate range characteristically follow the typical pattern of mammalian mortality, with very young and old having the highest rates of mortality during winter, with poor condition as the common symptom (Klein and Olson 1960; Klein 1970, 1981; Lowe 1969; Mitchell et al. 1971; Mitchell and Staines 1976). However, when food becomes limiting, because of high densities, deterioration and over-utilisation of the range, or any other reasons, then losses become

excessive and may include adults of intermediate age (Klein and Olson 1960; Clutton-Brock *et al.* (1982a). Although assessments of infant and juvenile mortality could not be made (but in view of their inferior fat reserves are considered to be at least as high as for adults), the high proportion of prime-aged males and females that died from starvation (Fig. 4.34) therefore indicates that bushbuck were over-abundant during the period of study at Weza. This is supported by the high incidence of winter mortality among marked animals (33% in 1983) that occupied preferred habitats where malnutrition was probably less rife than in more marginal or inferior areas (see Chapters Seven and Nine). The occurrence of most natural mortalities during the winter and early spring, together with the depleted fat reserves of bushbuck that were culled (18% of all bushbuck sampled had fat deposits comparable to those from animals that had died from starvation/exposure), or found dead at this time (Tables 4.10 and 4.11), strongly suggest winter nutrition as the main limiting factor. These conclusions are considered further in Chapter Ten).

Duiker mortality patterns appear to differ markedly from those of bushbuck, but because of the high proportions of duiker that died from unnatural and unknown causes (Fig. 4.37), and at unknown times of the year, conclusions regarding mortality in this species must, by necessity, be somewhat speculative. With the exception of two duiker deaths (both infants) in September 1980, there was no evidence of mortality caused directly by malnutrition, and none of the duiker that were culled were debilitated; all had % DM values in excess of 30% throughout the year. These findings are in general agreement with those of Schmidt (1984b) who concluded that duiker inhabiting plantations retain reasonable fat deposits throughout the winter.

Irrespective of cause of death, males outnumbered females by almost three times in the number of carcasses found. While this sample suggests sex differential mortality, none of the factors influencing higher male mortality rates detailed above are considered responsible for

this disparate ratio. Several authors have shown that male biased mortality may be due to selective predation (Wright 1960; Mitchell et al. 1965; Hirst 1969a; Pienaar 1969b; Schaller 1972; Smuts 1974b, 1976a; Joubert and Bronkhorst 1977; Anderson 1978) but it is difficult to envisage how male duiker would be more susceptible to predation when both sexes have identical patterns of social and spatial organisation (see Chapter Eight). In some ungulate species, young bachelor males may be forced, by territorial males, into inferior habitats where they may suffer relatively greater mortality than females through increased nutritional and social stress, and predation pressure (Jarman and Jarman 1973; Jarman 1974; Crowe and Liversidge 1977; Leuthold 1978a) but again, this is considered an unlikely cause in duiker since adults of both sexes exclude members of the same sex from their territories (see Chapter Eight). Consequently, the higher incidence of male carcasses collected in this study is probably of no biological significance but rather an artefact of sampling. Population sex ratios derived from culling and from censuses (see Chapter Ten) concur with this conclusion.

Although duiker carcasses were collected in a somewhat haphazard manner, the age structure of these and of marked animals that "disappeared" from their territories suggest that mortality rates are not age-related in the population at Weza. Ignoring losses through disease, predation or unnatural causes (all of which are considered to be fairly slight, see above) this would infer that, at certain times, food quality and quantity is totally inadequate. Deposited fat reserves (which could rarely be assessed from carcasses) of culled animals demonstrate that food is not limiting on a seasonal basis. However, inadequate nutrition may result from adverse changes in plant succession (Klein 1970) which in turn could be a consequence of forestry practices. The impact that silvicultural and harvesting activities, which occur throughout the year, may have on duiker at Weza is considered in detail in Chapters Seven and Ten.

CHAPTER FIVE
REPRODUCTION

5.1 INTRODUCTION

Population stability, decline or growth is determined by the interactive influences of natality, mortality, immigration and emigration. Since reproductive success depends on a number of physiologically and environmentally related factors, these need to be recognised and clearly understood before any wildlife population can be effectively managed. Further, once qualified, these factors then facilitate comparisons of the reproductive performances of populations under differing environmental conditions and at different intensities of management.

Attwell (1977) has identified a number of aspects of reproduction in the female which are subject to variation. Several of these also vary within the male but are usually less obvious or have a less pronounced effect on recruitment because the factors affecting overall reproductive success differ between the sexes. The energetic costs of reproduction (including gestation, lactation and parental care) are usually much higher in females, and consequently their reproductive success is largely limited by the availability of adequate resources. In contrast, the reproductive success of males is usually limited by access to fertile females (Clutton-Brock et al. 1982a)

The first of these variable aspects is the age at attainment of puberty and/or sexual maturity, which may have a pronounced effect on the reproductive potential of a population (Hanks 1979) and provides a particularly sensitive indication of population performance (Thomas 1983). Numerous studies have shown that age at puberty is largely influenced by body size and condition, and hence by rates of growth (Sadleir 1969a, 1969b; Verme 1969; Lincoln et al. 1970; Youngson 1970; Mitchell 1973; Mitchell and Brown 1974; Wegge 1975; Staines 1978; Hamilton and Blaxter 1980; Mitchell and

Crisp 1981; Mitchell et al. 1981; Albon et al. 1983).

A second aspect of reproduction that shows considerable variation concerns the fecundity rate of a female, which is measured as the number of live births she produces over an interval of time, generally one year (Caughley 1977). Again, this may depend upon the size and condition of the mature female, which in turn are affected by the quality of the animals' range, population densities and/or previous reproductive status (Verme 1965; Sadleir 1969b; Lowe 1969, 1971; Klein 1970; Mitchell 1973; Mitchell and Brown 1974; Guinness et al. 1978c; Mitchell and Crisp 1981; Mitchell et al. 1981; Mundinger 1981; Albon et al. 1983). Even factors as subtle as the sex of the mother's previous young may influence fecundity (Guinness et al. 1978a; Clutton-Brock et al. 1983).

The onset and duration of breeding each year may be affected by a variety of factors, yet a knowledge of these events is crucial to the reliable estimation of densities and population structure, and to an evaluation of the optimal times and levels of exploitation. Seasonal breeding in ungulates has evolved so that births occur when conditions are optimal for the survival of both mother and young (Sadleir 1969a), and factors responsible for the initial onset of breeding (proximate factors) and the timing of the resultant births (ultimate factors) have been comprehensively reviewed by Sadleir (1969a, 1969b), Spinage (1973b) and Anderson (1979). Proximate and ultimate factors are most obvious in those species that have a highly restricted, synchronised season of birth (e.g. wildebeest - Estes 1966, 1976; Attwell 1977; Estes and Estes 1979). Seasonal breeding may however vary between populations in different localities (e.g. impala - Skinner 1971a, 1978; Anderson 1975; and eland - Skinner and van Zyl 1969), or between years when environmental conditions, and hence proximate cues, fluctuate (Skinner et al. 1974). Where species show aseasonal breeding, this usually infers that their nutritional requirements remain relatively constant throughout the year (Skinner et al. 1974; Leuthold and Leuthold 1975a). The

timing and duration of reproduction may also be influenced, albeit to a much lesser extent, by the age of the females breeding (Simpson 1968; Mitchell and Lincoln 1973; Underwood 1975; Allen-Rowlandson 1980), previous reproductive history, including the sex of the last offspring (Clutton-Brock et al. 1983), mortality rates of offspring during the previous year (McGinnes and Downing 1977) and nutrition during pregnancy (Verme 1965, 1969; Skinner and van Zyl 1969). This last aspect may have a marked effect on the development and subsequent survival of the offspring (Klein 1970; Mitchell 1971,1973; Verme 1962 cited in Mundinger 1981; Verme 1969; Wegge 1975; Thorne 1976; Guinness et al. 1978b), and in turn will directly affect another variable, namely the duration of lactation, which may also influence or be influenced by subsequent reproduction (Hall-Martin et al. 1977; McGinnes and Downing 1977; Clutton-Brock et al. 1983). One final aspect of female reproduction that may show variation concerns reproductive senescence, but this aspect is of minor importance since with increasing age and hence mortality, breeding females contribute less and less to a population's power of increase (Cole 1954 cited in Mentis 1972; Hanks and McIntosh 1973).

Methods employed by biologists studying these aspects vary, and results emanating from these different sources of data collection may not always be directly comparable. One of the most accurate means of collecting reproductive data is by direct observation (this does not necessarily include the casual observations of early natural historians however). Numerous studies have detailed the onset and duration of the rutting or mating season (e.g. Spinage 1969a; Jungius 1970; Lincoln and Guinness 1973) and the calving season (Arman 1974; Clutton-Brock and Guinness 1975; McGinnes and Downing 1977; Arman et al. 1978; Sekulic 1978; Guinness et al. 1978c), and by the difference in the timing of these two events, the gestation period (Watson 1969; Skinner and van Zyl 1969; Guinness et al. 1971; David 1975; Jeffery 1979). Field methods have also been used to determine the age of attainment of sexual maturity, conception and parturition rates, the duration of lactation, and recruitment rates (e.g.

Bergerud 1964; Goddard 1970b; Rowe-Rowe and Bigalke 1972; Follis and Spillett 1974; Langman 1977; Mundinger 1981). However, in many of these instances the animals under study were either exceedingly tame or intensively managed, or alternatively, one specific aspect of reproduction was being investigated. For population assessment purposes, and where conditions are less optimal, records from live animals may be inadequate (Sinclair and Grimsdell 1982) and under these circumstances, the only practical means of collecting sufficient data is by post-mortem examinations (e.g. Hanks 1972c; Haugen 1974; Nichols 1978; Salwasser and Holl 1979; Thomas 1983). Such an approach was adopted in this study although where relevant, supplementary data were included from field sightings. The emphasis of this aspect of the study was geared towards an assessment of population performance that would be of value to management. Consequently, established and recognised basic techniques have been employed in favour of more elaborate or refined methods such as spermatogenic activity, sperm motility, fructose and citric acid concentrations and hormone assays, that are oriented more towards physiological studies (e.g.Johnson and Buss 1967a,1967b; Skinner 1971a, 1971b; Skinner and Huntley 1971a, 1971b; Skinner et al. 1971; Fairall 1972; Bramley and Neaves 1972; Mirarchi et al. 1977a; Plotka et al. 1977).

Discussions in this chapter are confined to reproduction per se; the implications of these results in terms of population performance and management are considered in Chapter Ten.

5.1.1 Previous Studies of Reproduction in Bushbuck and Duiker

5.1.1.1 Sources of information and definitions

The reproductive biology of the bushbuck has been examined in some detail in three previous studies (Allsopp 1970; Morris 1973; Simpson 1974c) while the major published accounts of reproduction in the duiker have largely been

based on material obtained from tsetse fly control operations (Wilson and Clarke 1962; Wilson and Child 1964; Wilson and Roth 1967). In this review, supplementary information on the reproduction of these two species has been collated from published records of captive animals and from faunal surveys conducted in various regions of the sub-continent. Records from this latter source in particular, have often been based on casual observations and consequently are not necessarily as accurate or comprehensive as those obtained by more exacting means. In addition, as Sadleir (1969a) noted, definitions of various reproductive events have differed between authors, a notable example being the term "sexual maturity". This has been interpreted as the earliest age at which germ cells are released (e.g. Morris and Hanks 1974), the age at which an animal commences breeding (e.g. Dittrich 1972) or the age at which a female becomes primiparous (e.g. Allsopp 1970; Dittrich 1970). Occasionally, the term has been applied to females breeding for the first time but which are already pregnant (e.g. Child and Wilson 1964; Wilson and Child 1964; Wilson and Roth 1967); this differs from the definition of when a female commences breeding (i.e. age at first conception) because it includes a variable and often unspecified length of pregnancy. Since these alternative meanings of the same reproductive terms may conceal or exaggerate population differences in reproductive performance, they have, where possible, been avoided in this study. This has necessitated alterations to published definitions, and on occasion, to the ages at which specific events occur, but following the definitions given below, has provided a more consistent approach which facilitated comparisons at the population level. In this study, the term "puberty" is considered as the age at which gamete production commences, while attainment of "sexual maturity" corresponds to the earliest age at which mating under normal conditions occurs. In many ungulate species that are polyoestrous, puberty in females usually coincides with, or is closely followed by, sexual maturity (Morris 1973; Anderson 1978; Allen-Rowlandson 1980) and in such instances these terms may be used synonymously. In contrast, pubertal males rarely have an opportunity to mate because of competition from

older, more dominant males and there is therefore a delay between puberty and the onset of sexual maturity (Altmann 1960; Estes 1969; David 1973; Sinclair 1974; Spinage 1974; Laws et al. 1975; Leuthold 1977). The most common means of determining when males become sexually (and sociologically) mature is by behavioural observations in the field (e.g. Spinage 1969a; Leuthold 1970a; Jarman and Jarman 1973; Bergerud 1974; Buechner 1974; Grubb 1974b,1974c: Warren 1974; Lewin 1978; Jarman 1979; Allen-Rowlandson 1980; Clutton-Brock et al. 1982a; Owen-Smith 1984), but because of flight distances, limited visibility and other restrictions detailed in Chapter Eight, these could rarely be maintained for adequate periods of time at Weza. Consequently with reference to males, the term sexual maturity has been avoided in this study; instead animals older than the age at which puberty is attained are referred to as "postpubertal" or "adult". The term "fertility" refers to the ability of an animal to produce young. All other terms are considered to be unambiguous. More extensive changes to published data have been necessary for duiker and these are detailed in Section 5.1.1.3.

5.1.1.2 Bushbuck

5.1.1.2.1 Gestation period

Estimates of the gestation period of this species vary from approximately 165 days (Allsopp 1971; Mentis 1972) to 225 days (Kenneth and Ritchie 1953), as shown in Table 5.1. Dittrich's (1972) data were based on records of captive bushbuck and a mean value of 180 days has generally been accepted as the most accurate estimate (Allsopp 1970, 1971; Morris 1973; Morris and Hanks 1974; Simpson 1974c; von Ketelhodt 1976).

5.1.1.2.2 Puberty and sexual maturity

The mean age at puberty in bushbuck males has been estimated at 10,5 months when animals had a combined testes mass of 15g and a mean seminiferous tubule diameter of 140 μm

TABLE 5.1 Gestation periods quoted for bushbuck.

Gestation period (days)	Source
c. 165	Mentis (1972)
165	Allsopp (1971)
180	Allsopp (1971)
178	Dittrich (1972)
179	Dittrich (1972)
182	Dittrich (1972)
180	Zaloumis and Cross (1974)
180 - 225	Kenneth and Ritchie (1953)
c. 210	Stevenson-Hamilton (1912) cited in von Ketelhodt (1976)
214 - 225	Kenneth (1947) cited in Brand (1964)
220	Morris and Jarvis (1959)
c. 220	Walker (1975)
c. 225	Crandall (1964)

(Morris 1973; Morris and Hanks 1974). Allsopp (1970) also found active spermatogenesis in males of 12 months, and Simpson (1974c) concluded that males in his population reached puberty between the ages of 10 and 19 months when testes growth was most pronounced. Morris (1973) illustrated the growth and development of the male gonads with age.

Morris (1973) and Morris and Hanks (1974) estimated that puberty in female bushbuck occurred at a mean age of 11 months, and extrapolation of foetal ages from 14 month old pregnant females confirmed that both puberty and sexual maturity occurred before females reached one year of age. Using broad age classes, Allsopp (1970) recorded pregnancy in one 12 month old female and thereafter in all of the 18 month to 30 month old females he examined, while Simpson (1974c) also found an unspecified number of 14 months old females to be pregnant. Unfortunately, although both of these authors

determined foetal ages for assessments of seasonal breeding, neither subtracted these where relevant to provide ages at first conception, and Wilson and Child (1964) merely reported that the youngest female found to be pregnant was 19 months old. Records from captive animals also suggest that sexual maturity is attained between 12 and 18 months of age. Jacobsen (1974) notes that a female came into oestrus for the first time when 16 months old, while the age at first conception has been recorded as 18 to 19 months (Dittrich 1972; Mentis 1972), but as early as 11 to 12,5 months (von Ketelhodt 1976).

5.1.1.2.3 Age at first parturition

Surprisingly none of the authors involved in detailed reproductive studies of this species determined the precise age at which bushbuck give birth for the first time, yet all had foetal age data at their disposal. Addition of the gestation period to the mean age at puberty determined by Morris (1973) would indicate a minimum age at first parturition of 17 months, but direct evidence is confined to records of captive animals (which may or may not be influenced by management practices such as the timing of the introduction of a suitable mate etc.). These records suggest that bushbuck lamb for the first time at ages varying from 17 to 19 months (Morris 1973; von Ketelhodt 1976), to 24 to 27 months (Allsopp 1970; Dittrich 1970, 1972; Mentis 1972).

5.1.1.2.4 Pregnancy and lactation

Morris (1973) described and illustrated the development of the ovaries, uterus and udder with age and the associated changes in these tissues during pregnancy and lactation. Regressing corpora lutea (corpora albicantia) were difficult to distinguish from those that were active, and Morris (1973) found that evidence of previous ovulatory activity (corpora nigra) did not remain indefinitely in the ovary, and could not be detected in over 32% of the mature ovaries he

examined. Simpson (1974c) recorded that ovulation occurred from the left and right ovaries with equal frequencies, but that implantation was always ipsilateral to ovulation in 39 pregnancies. Twin foetuses were recovered by Dittrich (1970), and all available evidence from foetuses and infants have indicated a sex ratio close to unity (Brand 1963; Wilson and Child 1964; Morris and Hanks 1974).

Morris (1973) found five of the 45 pregnant females (11%) in his sample were lactating, while the proportion of females that were pregnant during his six months of sampling apparently varied from 28% to 89% which led him to conclude that a certain degree of seasonality of breeding occurred in this population. Re-examination of his raw data gives contrary results however, and these will be detailed in the Discussion. Overall, his data indicated a mean prevalence of pregnancy of 36,8% (46% if only mature females are considered). Allsopp (1970) quoted a 68% prevalence of pregnancy for his population in Kenya, where a further 23% of the 35 mature females were lactating , and thus at least 91% of the sample was actively breeding during the year. Simpson (1974c) found pregnancy rates of 67% (n = 52) and 57% (n = 453) in two different populations, and when the proportion of lactating females were added to these, 83% and 78% of the females in these respective populations were breeding. The proportion of mature females that were pregnant and/or lactating in a third population was 89% (n = 18). Sixty percent of the 25 mature females examined by Wilson and Child (1964) were pregnant and a further 12% were lactating.

The mass of neonates has been recorded by several authors and these are detailed in Table 5.2. Allsopp (1971) used a mean mass at birth of 4 175g for the calculation of the foetal growth velocity (required for the determination of foetal age, Huggett and Widdas 1951) while Morris (1973) and Morris and Hanks (1974) relied on a birth mass of 3 400g for the same equation, and Simpson (1974c) did not specify what parameters were used in his study. Allsopp (1970) provided evidence of lactation continuing for five months postpartum, and quoted other sources where the duration of lactation had

been estimated at approximately eight months. Kingdon (1982) stated that for much of this time the infant is hidden and only begins to follow the mother when it is nearly four months old.

TABLE 5.2 Mass of newborn bushbuck.

Mass of neonate (g)	Source
2 664 (female)	Wilson and Child (1964)
2 778 (male)	Wilson and Child (1964)
2 863 (female)	Wilson and Child (1964)
3 118 (male)	Wilson and Child (1964)
3 203 (female)	Wilson and Child (1964)
3 628 (female)	Wilson and Child (1964)
3 325 (male)	Dittrich (1969)
3 375 (female)	Dittrich (1969)
3 570 (female)	Dittrich (1969)
4 175 (male)	Dittrich (1969)
3 400	Morris (1973)
c. 3 400	Morris and Hanks (1974)

5.1.1.2.5 Senescence

The absence of any evidence of sexual senescence in either males or females has been reported by Simpson (1974c) and Morris (1973). The latter author did, however, find a partial degeneration of the seminiferous tubules in a 114 month old male, but normal spermatogenesis was evident elsewhere in the testis, implying that fertility had not been impaired.

5.1.1.2.6 Parturition intervals

Simpson (1974c) concluded that parturition intervals of 180 days were realised in the population he was studying, but his reasoning for this conclusion was extremely speculative

and based merely on one culled female that had been lactating for an unknown duration and that was in oestrus. Allsopp's (1970) method of determining parturition intervals was also highly subjective since he assumed that the duration of lactation was six to seven months, and subtracted a mean foetal age of 75 days from this to obtain a mean postpartum interval of 105 to 135 days. This interval, added to the gestation period, yielded a mean parturition interval of 285 to 315 days. Morris (1973) adopted a more objective approach by determining the ages of an infant and the foetus of the mother accompanying it; the difference in these ages provided the interval between pregnancies of 45 days, which, combined with the gestation period indicated a parturition interval of approximately 225 days. Other parturition intervals obtained from captive animals are presented in Table 5.3. Only two intervals of under 200 days have been recorded, one of which equals the accepted gestation period of this species (Dittrich 1974), implying an immediate postpartum conception (Dittrich 1968). The other interval of 166 days led Mentis

TABLE 5.3 Parturition intervals recorded from captive bushbuck. (Values marked with an asterisk denote successive births to the same female).

Parturition Interval	Source	Parturition Interval	Source
247	Morris (1973)	251*	von Ketelhodt (1976)
247	Morris (1973)	242*	von Ketelhodt (1976)
252	Morris (1973)	256*	von Ketelhodt (1976)
334*	Mentis (1972)	239*	von Ketelhodt (1976)
166*	Mentis (1972)	242**	von Ketelhodt (1976)
c. 240	Mentis (1972)	245**	von Ketelhodt (1976)
269*	Dittrich (1974)	269	von Ketelhodt (1976)
396*	Dittrich (1974)	225	Kingdon (1982)
180*	Dittrich (1974)		
247*	Dittrich (1974)		
241*	Dittrich (1974)		
385*	Dittrich (1974)		

(1972) to suggest a gestation period of 165 days or less (see Table 5.1).

5.1.1.2.7 Seasonality

Several authors have concluded that breeding is confined to certain favourable times of the year in some areas (e.g. Duckworth 1948; Kirby 1899 cited in Brand 1963; Asdell 1964; Fairall 1968) while it has also been suggested that bushbuck breed throughout the year but have distinct birth peaks at specific times, usually coincidental with the onset of rains during the summer months (Smithers 1966, 1971; Thomson 1972 cited in Morris and Hanks 1974; Zaloumis and Cross 1974). Using foetal ages to determine the temporal distribution of conceptions and births, the authors of all the detailed studies of bushbuck reproduction were of the latter opinion, (Allsopp 1970, 1971; Morris 1973; Morris and Hanks 1974; Simpson 1974c), while out of a total of 29 sightings of infants, Odendaal and Bigalke (1979a) found distinct peaks in the number of young bushbuck seen during April, August and November. Simpson (1974c) noted a decline in testes mass during the two peak mating periods determined from foetal age.

The absence of any seasonal peak in reproduction has been reported by Ansell (1960a, 1960b), Verschuren (1958) cited in Asdell (1964), Brand (1963), Mentis (1973b), Jacobsen (1974) and Walker (1975) and in captivity breeding is also evident throughout the year (Zuckerman 1953 cited in Mentis 1972; Jarvis and Morris 1961; Brand 1963; Crandall 1965; Dittrich 1970; von Ketelhodt 1976).

5.1.1.3 Duiker

5.1.1.3.1 Gestation period

Published accounts of the gestation period of this species show considerably more variation than those for bushbuck (Table 5.4) and range from approximately 90 days

(Sommerlatte 1979 cited in Smithers 1983) to 210 days (Zaloumis and Cross 1974). Doubts have been expressed regarding the accuracy of some of these values (Roberts 1951) and since gestation periods are rarely influenced by environmental conditions (Sadleir 1969a), it would appear that such variation is probably due to errors of estimation.

Clearly, the adoption of an incorrect value could seriously influence assessments of the seasonality of breeding, intervals between lambing, and the ages at first conception and parturition. The more recent reports suggest a period of closer to seven months (Sikes 1958; Morris 1965 cited in Keymer 1969; Mentis 1972) and the value of 210 days

TABLE 5.4 Gestation periods quoted for common duiker.

Gestation period (days)	Source
c. 90	Sommerlatte (1979) cited in Smithers (1983)
120	Dorst and Dandelot (1970)
120	Kenneth (1947) cited in Brand (1963)
120	Kenneth and Ritchie (1953)
c. 120	Stevenson-Hamilton (1912) cited in von Ketelhodt (1977)
121	Morris and Jarvis (1959)
123	Jennison (1927) cited in Kenneth and Ritchie (1953)
c. 135 - 165	Mentis (1972)
120 - 210	Roberts (1951)
c. 170	Sikes (1958)
191	V. Wilson (pers. comm.)
196	Morris (1965) cited in Keymer (1969)
c. 210	Mentis (1972)
210	Wilhelm (1933) cited in Kenneth and Ritchie (1953)
210	Zaloumis and Cross (1974)

quoted by Zaloumis and Cross (1974) has been used by von Ketelhodt (1977) in his determination of parturition intervals for this species. Recent unpublished values based on captive animals provide an average period of 191 days with an upper limit of 204 days (V.J. Wilson pers. comm.). Data from other duiker species also suggest a gestation period in excess of six months. These include the blue duiker - 205 days (Heinroth 1908 cited by Dittrich 1972), the red-flanked duiker - 223 to 245 days (Dittrich 1972) and the bay duiker - 256 days (Dittrich 1970). Other small antelope species also having gestation periods close to 200 days include:

Steenbok (Raphicerus campestris) : 168-177 days (Bigalke 1963)
Steenbok (Raphicerus campestris) : 210 days (Morris and Jarvis 1959)
Springbok (Antidorcas marsupialis): 171 days (Morris and Jarvis 1959)
Kirk's dik-dik (Madoqua kirkii) : 169-174 days (Dittrich 1970)
Thomson's gazelle (Gazella thomsoni): 180 days (Leuthold 1972)
Klipspringer (Oreotragus oreotragus): 214 days (Kenneth and Ritchie 1953)
Oribi (Ourebia ourebi) : 217-220 days (Dittrich 1974)

Since the length of gestation is closely correlated to the mass of the adult female (Sadleir 1969a, 1972, 1973), these data further indicate that a gestation period approximating the upper range of values in Table 5.4 is more probable for common duiker, and the calculated average value of 191 days given by Wilson (pers. comm.) has therefore been used in this study. Wherever possible, this estimate has also been used to replace the lower values used by previous authors in determining ages at sexual maturity etc. detailed below.

5.1.1.3.2 Puberty and sexual maturity

There is no direct evidence indicating age at attainment of puberty in this species, while indirect evidence has been unsatisfactory in view of the conflicting observations on the

length of the gestation period (see above) and the questionable accuracy of the age determination criteria developed by Riney and Child (1960) that has been used in most estimates of sexual maturity (Mentis 1972). In addition to the consistent use of a gestation period of 191 days, wherever possible ages have been adjusted in this review to conform with the comprehensive age determination criteria detailed by Wilson et al. (1984). As a result of these adjustments, many of the ages provided here differ from those published by the original authors.

Wilson and Roth (1967) found the the earliest age at which females were pregnant was 20 to 24 months during the first year of culling, but had lowered to 9 to 10 months one year later, possibly in response to increased hunting intensity and the resultant decrease in intra- and inter-specific competition. Females already pregnant at the age of 9 to 10 months were also collected by Child and Wilson (1964). Assuming a gestation period of 191 days, two captive duiker conceived for the first time at 13,5 months and 5,5 months (Child and Wilson 1964 and Ansell 1963 respectively). This latter record represents the earliest age of sexual maturity published for this species.

5.1.1.3.3 Age at first parturition

Dasmann and Mossman (1962a) suspected that duiker lambed for the first time when one year old, and although Ansell (1963) has confirmed that females may become primiparous at this age, records from other captive animals suggest that most females giving birth for the first time do so at a somewhat later age of 18 to 20 months (Wilson and Clarke 1962; Mentis 1972).

5.1.1.3.4 Pregnancy and lactation

Although ovulation occurs with equal frequency in both left and right ovaries, (Symington and Paterson 1970),

implantation is confined to the right uterine horn of this species (Child and Mossman 1965; Symington and Paterson 1970; Smithers 1971). Earlier accounts suggested that twinning was a fairly common phenomenon (Shortridge 1934 cited in Keymer 1969; Stevenson-Hamilton 1947 cited in Smithers 1983; Ansell 1960a), but more recent authors are of the opinion that twins are a rare event (Wilson and Clarke 1962; Mentis 1972; Smithers 1983). Sikes (1958) described the birth of a grey duiker in detail, and the sex ratio of neonates examined by Wilson and Clarke (1962) was close to unity.

Wilson and Clarke (1962) ignored the incidence of lactation in their study, but their data suggest a prevalence of pregnancy of 51% (56% if only mature females are considered). Wilson and Roth (1967) included lactating females in their evaluation of breeding rates, and recorded a 52% prevalence of pregnancy (58% if females with deciduous dentition are excluded from the sample) during their first year of study. The proportion of mature females that were pregnant increased to 67% during the second year, after intensive hunting, but the proportion of all females that were pregnant remained unchanged at 52%. Within the adult segment of the population, the percentage of females that were either pregnant or lactating increased from 61% to 70% during the second year, while the proportion of juveniles and subadults that were either pregnant or lactating increased from 45% to 53%. Smithers (1971) found that only one out of 39 adult females collected throughout the year was not pregnant and/or lactating; thus 97,5% of the adult female population was reproductively active at this time.

The mass of newborn infants (160g to 190g) given by Wilson and Clarke (1962) and quoted by Smithers (1983) are incorrect and should read 1 350g, 1 600g, 1 600g and 1 900g (Wilson 1968). Wilson *et al.* (1984) gave the mean mass of male and female neonates as 1 510g and 1 640g respectively. Although captive duiker infants may be weaned at 10 weeks (Hopkins 1966), there are no records of the duration of lactation or concealment of the infant under natural conditions.

5.1.1.3.5 Parturition intervals

Child and Wilson (1964) observed an apparently pregnant female duiker with a lamb estimated at less than one month at foot, and found three of 26 females collected to be both pregnant and lactating. From these observations they concluded that the reproductive rate was unusually high in their heavily hunted area. However, Wilson and Clarke (1962) also found that of 48 gravid females, two were lactating and Fairall (1968) also recorded a lactating female carrying a large foetus. Although all of these authors implied that pregnancy and simultaneous lactation was an unusual event, parturition intervals from captive duiker suggest that a lactational anoestrus does not occur in this species and that parturition may be closely followed by conception. von Ketelhodt (1977) recorded 11 lambing intervals from 12 successive births between 1965 and 1974, and these ranged from 232 to 298 days, with an average interval of 259 days, while Mentis (1972) provided a single but similar value of 267 days obtained from another captive duiker.

5.1.1.3.6 Seasonality

Most authors have suggested that the duiker breeds continuously throughout the year (Shortridge 1934 cited in Brand 1963; Ansell 1960a, 1960b, 1963; Wilson and Clarke 1962; Pienaar 1963; Silberbauer 1965 cited in Mentis 1972; Keymer 1969; Dorst and Dandelot 1970; Smithers 1971, 1983; Mentis 1973a), but may exhibit peak births during the winter (Dasmann and Mossman 1962a; Smithers 1966; Fairall 1968) or summer months (Stevenson-Hamilton 1912 cited in Mentis 1972; Zaloumis and Cross 1974). Riney and Child (1960) presented evidence from skulls collected in tsetse control operations indicating two lambing peaks in mid-winter and mid-summer. In captivity, duiker breed throughout the year (Morris and Jarvis 1959) but again more births may occur during the summer months (Brand 1963).

5.2 METHODS

5.2.1 Source of Material

Material was obtained from 132 bushbuck (68 males and 64 females) and 118 duiker (61 males and 57 females) which were randomly culled within the extensive study area. Additional data were available from 36 bushbuck (19 males and 17 females) and 12 duiker (8 males and 4 females) that died from accidental or natural causes within both intensive and extensive study areas, and from 28 male bushbuck and 17 duiker (8 males and nine females) that were shot on adjacent farms during the hunting season (31st May to 31st August). Fifty-five percent of all the animals examined were collected during the first two years of study (Table 5.5).

TABLE 5.5 The numbers of bushbuck and duiker collected and examined each year from 1980 to 1984.

	1980	1981	1982	1983	1984	Total
Male busbuck	24	31	34	20	6	115
Female bushbuck	27	25	8	19	2	81
Male duiker	21	22	9	15	10	77
Female duiker	21	20	12	11	6	70
Total	93	98	63	65	24	343

5.2.2 Males

Once the carcass had been measured and weighed the testes and epididymides were removed by cutting through the scrotum and tunica vaginalis. The vas deferens was then trimmed level with the cauda epididymidis, and left and right testes and epididymides were weighed separately to 0,01g. In most instances a small portion of the testis, (i.e midway between the poles), and a distal portion of the caput

epididymidis were fixed in 10% buffered neutral formalin for subsequent histological examination. These specimens were dehydrated, embedded in paraffin wax, sectioned at 7µm and stained with Mayer's haematoxylin and 1% alcoholic eosin. The stained sections of testes were examined microscopically for the presence or absence of spermatogenesis. Testes were considered prepubertal if they showed no signs of spermatogenesis, and postpubertal after the commencement of spermatogenesis, when spermatids were visible in the lumina of seminiferous tubules. Confirmation of these categories was obtained by histological examination of the epididymides. Where autolysis did not prevent it, a mean seminiferous tubule diameter was determined for each testis by measuring the diameter of 30 circular tubules using a calibrated micrometer eyepiece.

Although the reproductive organs of four bushbuck and eight duiker collected towards the end of field work, and all those obtained from adjacent farms were dissected and weighed in an identical manner, these were not sectioned. Instead, epididymal smears (Kerr and Wilson 1967; Hvidberg-Hansen 1970; Mitchell 1973; Nichols 1978; Mitchell et al. 1981) were prepared from both fresh (animals from Weza) and fixed material (from hunts). Care was taken to avoid contamination between individuals, and where spermatozoa were not detected, smears from the testis were also examined (Kerr 1965).

5.2.3 Females

Prior to evisceration, the mammary gland was removed and its activity noted. Sub-samples of 57 bushbuck and 44 duiker udders from immature, non-lactating and lactating females were trimmed of excess skin, weighed to 0,01g and a portion fixed in 10% buffered neutral formalin. In obviously pregnant females, the site of implantation was noted before removal of the uterus and the presence of any corpus luteum visible in either ovary prior to sectioning was also recorded. Ovaries were weighed separately and fixed in 10% buffered neutral formalin, and after fixation, were sectioned

sagittally with a scalpel at approximately 2mm intervals. Cut surfaces were examined macroscopically (Cheatum 1949; Golley 1957) for corpora lutea and corpora albicantia and in those cases where either or both structures could not be identified macroscopically, 7µm sections of ovaries were examined histologically after routine embedding and staining with Mayer's haematoxylin and 1% alcoholic eosin. Similarly, sections of mammary gland were examined histologically when necessary to determine lactational status. Females were considered to be postpubertal and fertile by the presence of a corpus luteum or corpus albicans in the ovary, and/or by the occurrence of embryonic membranes, an embryo or a foetus and/or by the presence of milk in the udder (Lowe 1969; Mitchell 1973; Morris and Hanks 1974; Staines 1978; Mitchell and Crisp 1981; Mitchell et al. 1981). Females were considered to be breeding for the first time if they were pregnant with immature mammary glands.

All embryos less than 100g were weighed to 0,01g and foetuses were weighed to the nearest g. Foetal ages were determined using the Huggett and Widdas (1951) formula:

$$\sqrt[3]{M} = a(t-to)$$

where M = mass of foetus, a = specific foetal growth velocity, t = gestational age and to = a numerical estimate obtained from to = 0,2 x gestation period (for animals with a gestation length of 100-400 days). As in other similar studies (e.g. Mitchell and Lincoln 1973; Skinner and Hall-Martin 1975; Smuts 1975a;Anderson 1978; Allen-Rowlandson 1980), mean mass at birth and the gestation period were used to calculate "a". Foetal age could then be determined since;

$$t = \frac{\sqrt[3]{M} + ato}{a}$$

This age was subtracted from the date when the mother was killed to provide the conception date. The length of the gestation period was added to the conception date, thereby

producing the predicted birth date of the foetus. Where possible embryos and foetuses were sexed to provide information on natal sex ratios.

5.2.3 Field Observations

Supplementary reproductive data from field observations were largely confined to population structure estimates and breeding records of marked animals. The activities and associations of all observed animals were noted throughout the study (Chapter Eight).

Using the criteria detailed in Chapter Three, the sex and age of all individuals that could be positively identified during counts, culling operations and other routine activities were recorded during the first year of study when different sections of the extensive study area were surveyed for a minimum of five nights each month. Monthly proportions of observed infants were used to determine the temporal distribution of bushbuck and duiker births.

In subsequent years, observations were focused on 74 marked bushbuck and 38 marked duiker that had been captured or recaptured a total of 139 and 43 times respectively (see Appendix D). Using the experience gained from post-mortem examinations, immobilized females were recorded as having immature or mature udders, and in the latter instance were considered as not lactating if the gland showed no expressible milk. No attempt was made to immobilize obviously gravid females, and a restrained female was recorded as pregnant only if a foetus could be detected by gently palpating the abdomen. Estimates of ages at first parturition and lambing intervals were obtained from sighting records of marked animals, which were more comprehensive for bushbuck (see Chapters Seven and Eight, and Appendix D). Recaptured females afforded a means of checking earlier assessments of reproductive status derived from sightings of those individuals with their associates, and also provided

estimates of the duration of lactation (see below).

5.3 RESULTS

5.3.1 Male Bushbuck

5.3.1.1 Age at attainment of puberty

Spermatogenesis was evident in one (25%) of the 10 month old males and in all of the older bushbuck examined. Puberty (the earliest age at which sperm production had commenced in 50% of the individuals within that age class) was attained by 11 month old males (Fig. 5.1). Pubertal bushbuck had a combined testes mass of approximately 20g (Fig. 5.2), a mean seminiferous tubule diameter of 160µm (Fig. 5.3) and a mean body mass of 25,0 kg.

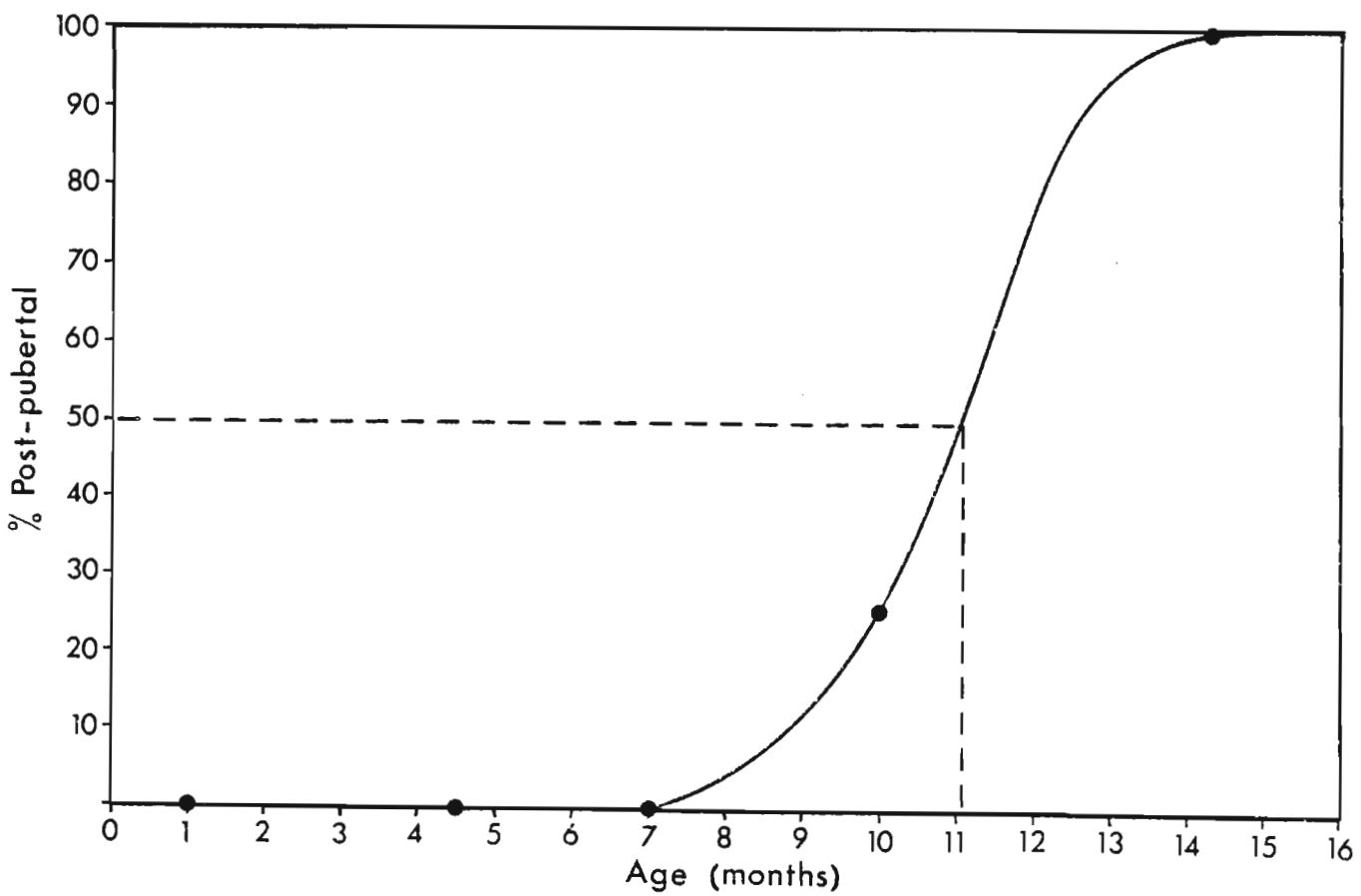


FIGURE 5.1 Mean age at puberty in male bushbuck (curve fitted by eye).

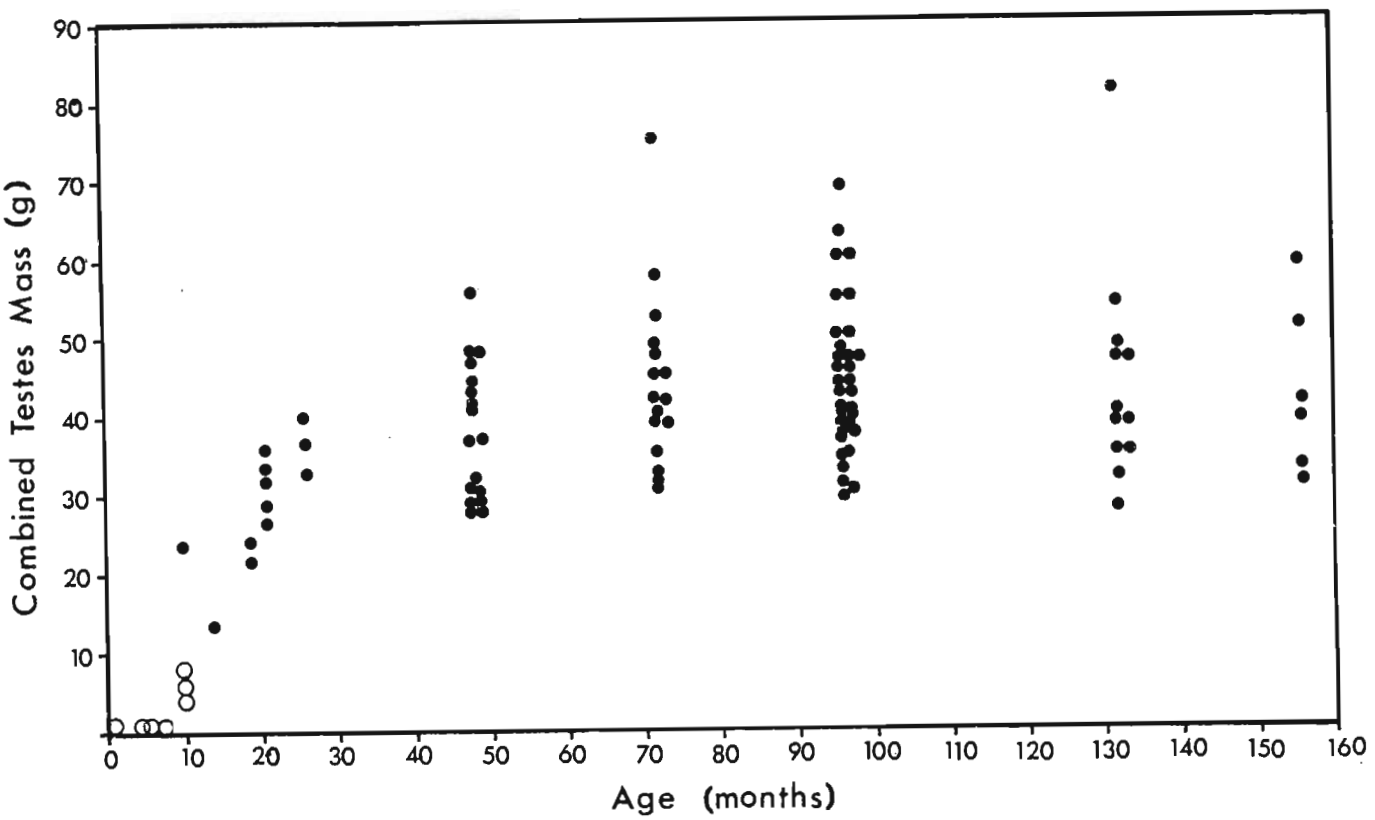


FIGURE 5.2 Growth in mass of testes in bushbuck with age (open circle - no spermatogenesis; closed circle - at least some through to full spermatogenesis).

5.3.1.2 Growth of reproductive organs with age

Growth in testes mass with age and changes in seminiferous tubule diameter with age are illustrated in Figs. 5.2 and 5.3 respectively. Prepubertal males characteristically had a combined testes mass of less than 10g and mean seminiferous tubule diameters smaller than 120µm. Growth of the testes continued in postpubertal males until about 48 months of age, when mean testes mass and seminiferous tubule diameter differences between these and all older males, and between each successive age classes, were not significant. Mean mass of paired epididymides showed a similar trend, except that those from 48 month old males were significantly lower than epididymides from all other adults ($t = 2,76$; $p<0,01$) and from those of 156 month old males ($t = 2,49$; $p<0,05$). There was a good relationship between combined testes mass and body mass and also between combined testes mass and seminiferous tubule diameter in

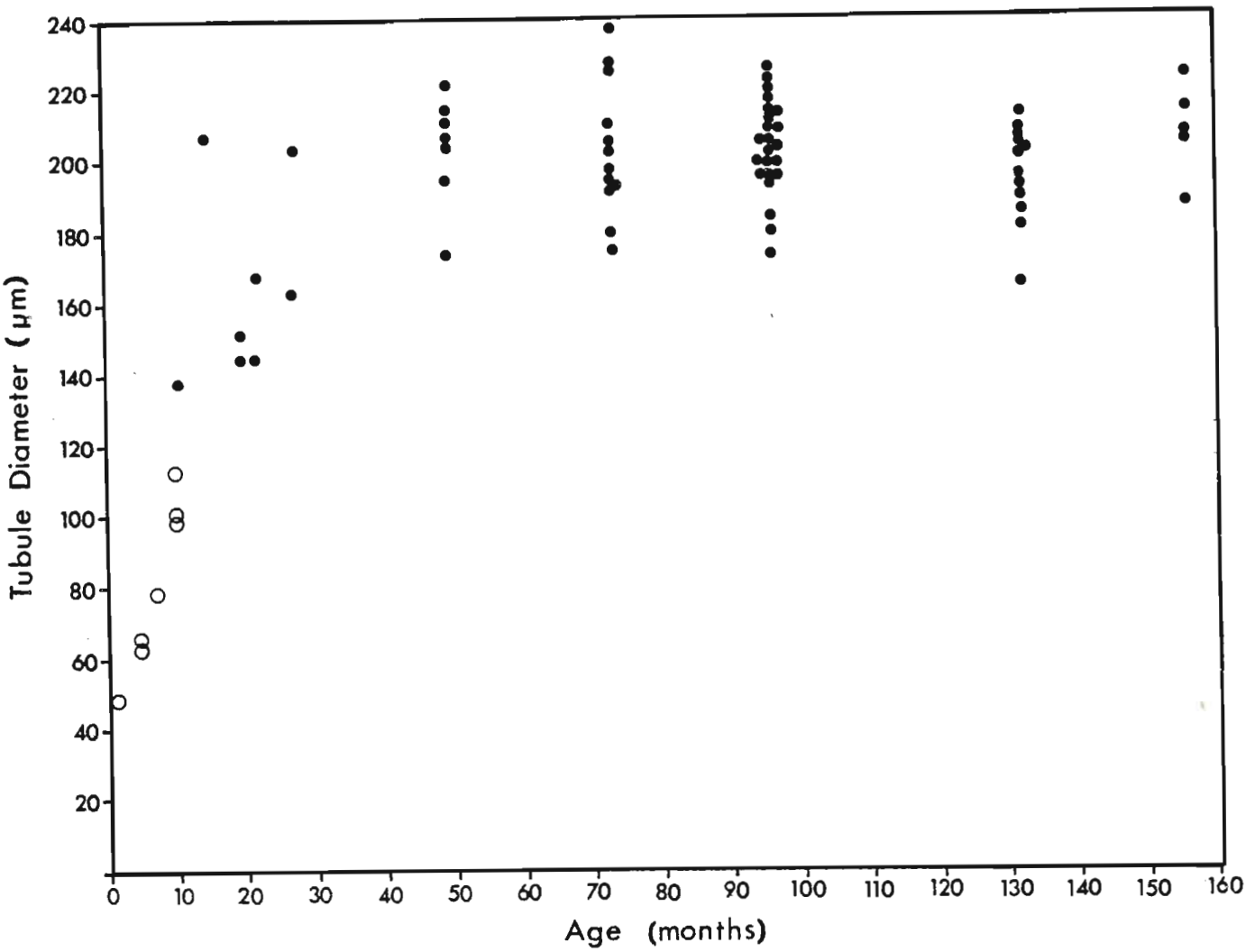


FIGURE 5.3 Variation in mean seminiferous tubule diameter of bushbuck with age (open circle - no spermatogenesis; closed circle - at least some through to full spermatogenesis).

prepubertal and postpubertal males (Figs. 5.4 and 5.5 respectively).

5.3.1.3 Seasonal changes in the reproductive organs

Only samples from those animals of 48 months and older were used as younger animals were still growing and could bias the sample. Monthly variations in testes mass of adult bushbuck are shown in Fig. 5.6, and when analysed on a seasonal basis, none of these were significant. Similarly there were no significant seasonal differences in the epididymides mass and in seminiferous tubule diameters.

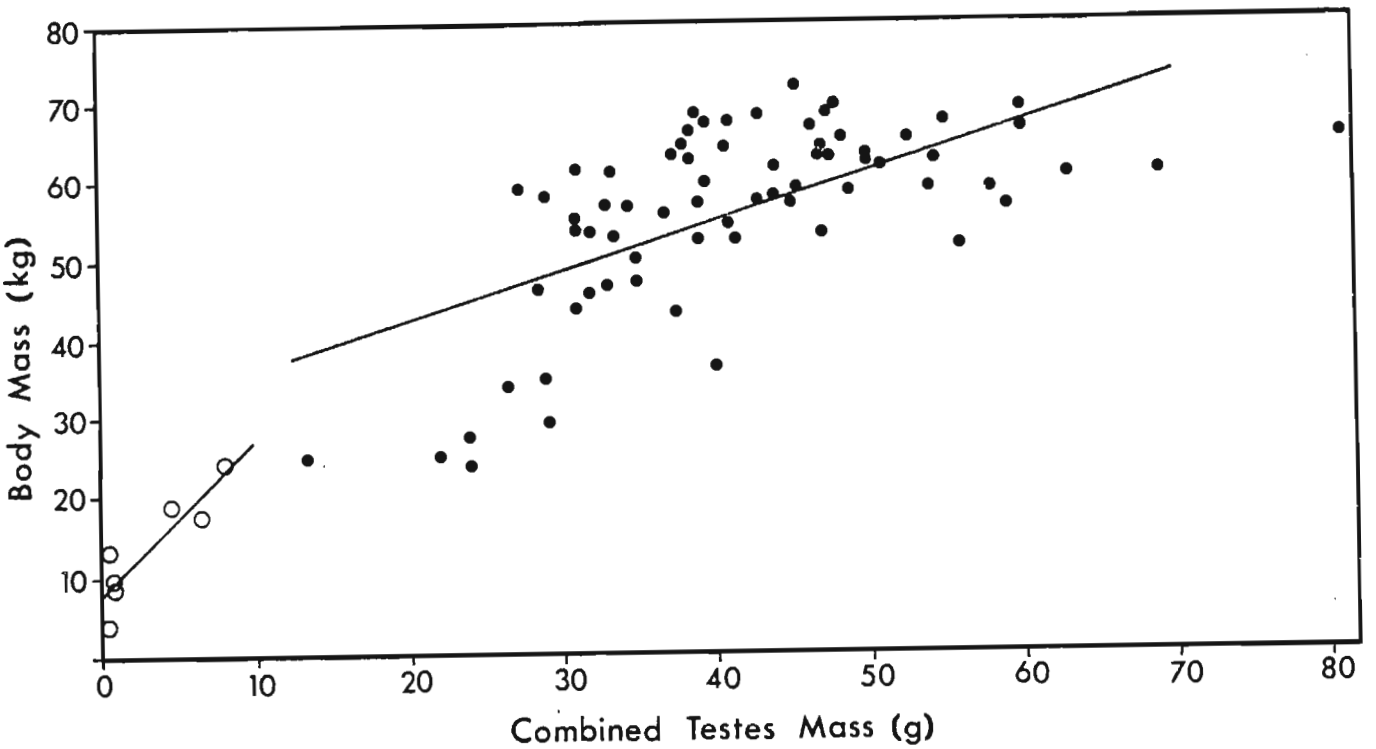


FIGURE 5.4 The relationship between combined testes mass and body mass in bushbuck. Prepubertal males (open circles) : y = 1,96x + 7,51 (r = 0,895; p<0,01). Postpubertal males (closed circles) : y = 0,62x + 29,77 (r = 0,625; p<0,001).

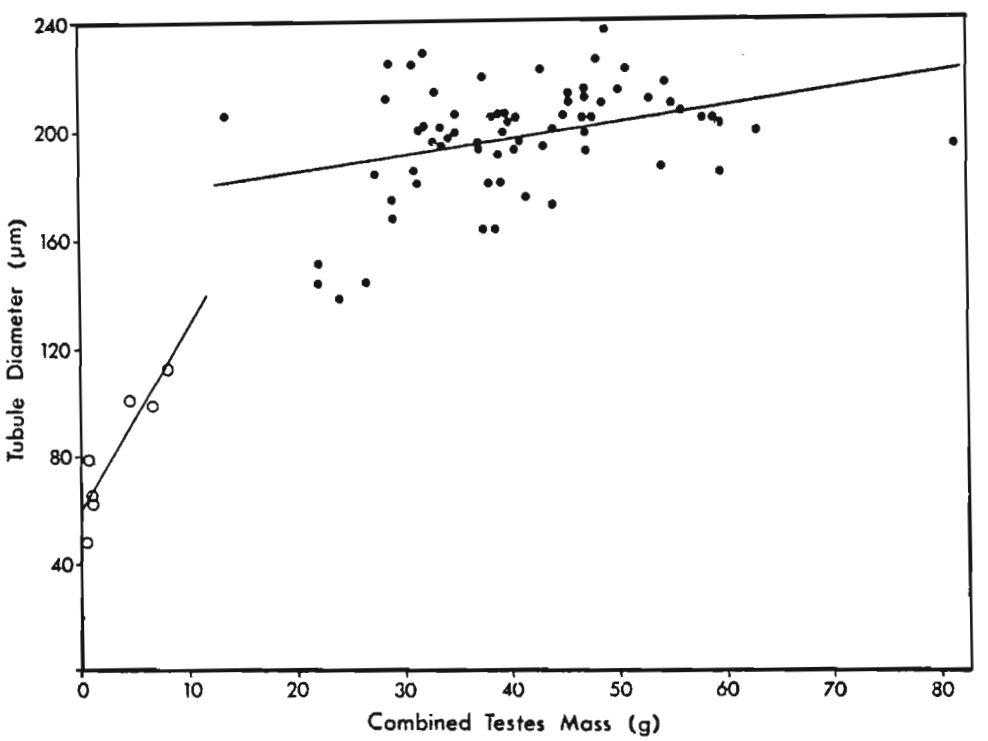


FIGURE 5.5 The relationship between testes mass and seminiferous tubule diameter in bushbuck. Prepubertal males (open circles) : y = 6,74x + 60,68 (r = 0,910; p<0,01). Postpubertal males (closed circles) : y = 0,61x + 172,04 (r = 0,342; p<0,01).

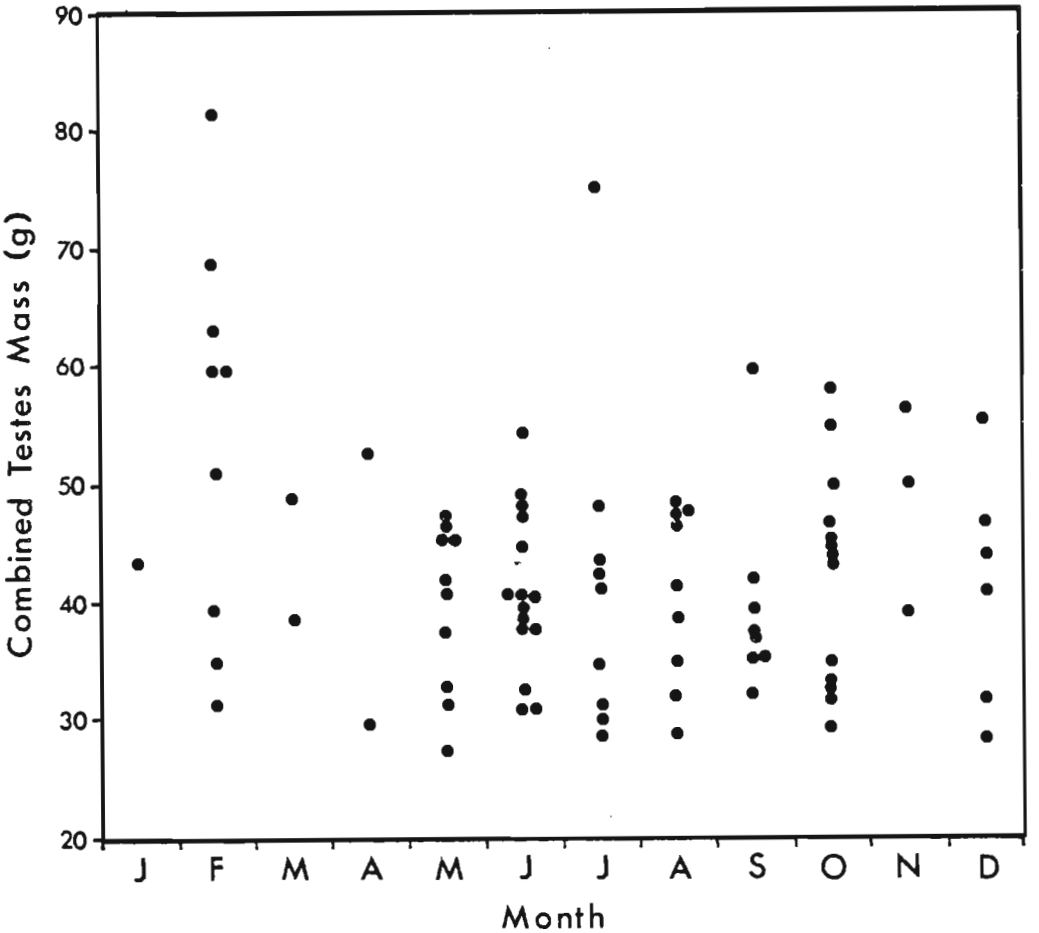


FIGURE 5.6 Monthly variation in combined testes mass of male bushbuck.

5.3.1.4 Senescence

The mean testes mass and seminiferous tubule diameters of the oldest males collected in this study did not differ significantly from those of younger adults. The detection of spermatozoa in the epididymides of all males older than 10 months was further indicative that physiological reproductive activity did not decline with age.

5.3.2 Male Duiker

5.3.2.1 Age at attainment of puberty

Spermatids were clearly visible in the lumina of seven (78%) 10 month old males, and the attainment of puberty was

determined at 9,5 months (Fig. 5.7). Pubertal duiker had a combined testes mass of approximately 19g (Fig. 5.8), a mean seminiferous tubule diameter of 153µm (Fig.5.9) and a mean body mass of 13,6 kg.

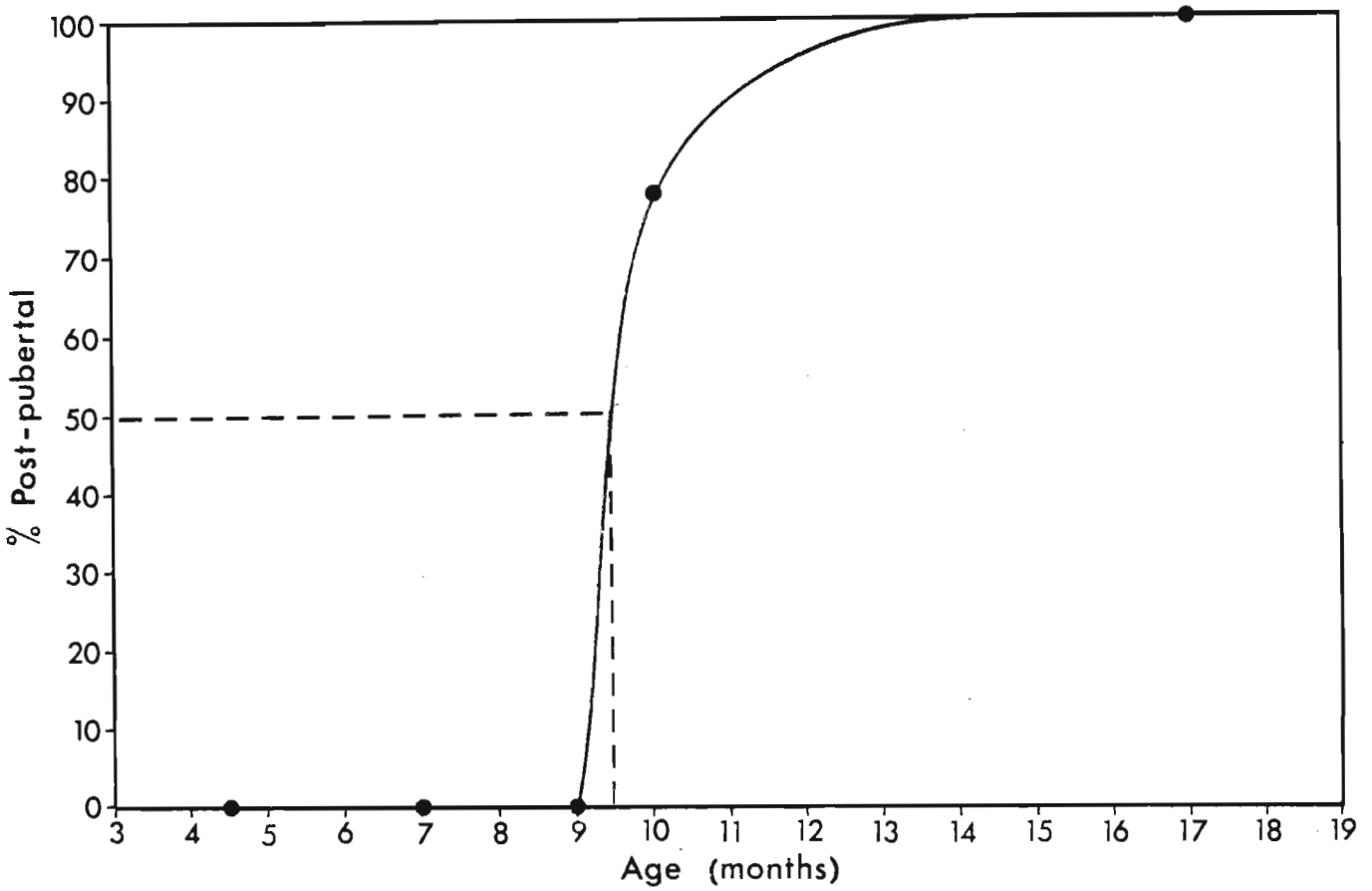


FIGURE 5.7 Mean age at puberty in male duiker (curve fitted by eye).

5.3.2.2 Growth of the reproductive organs with age

Growth in testes mass and changes in seminiferous tubule diameters with age are illustrated in Figs. 5.8 and 5.9 respectively. All of the prepubertal males examined had combined testes mass not exceeding 13g, and mean seminiferous tubule diameters smaller than 125µm. Growth in testes mass continued in postpubertal males until approximately 24 months of age, but differences in mean testes mass between successive age classes were not significant from the age of 20 months. Seminiferous tubule diameters and combined epididymides mass showed a similar trend with age.

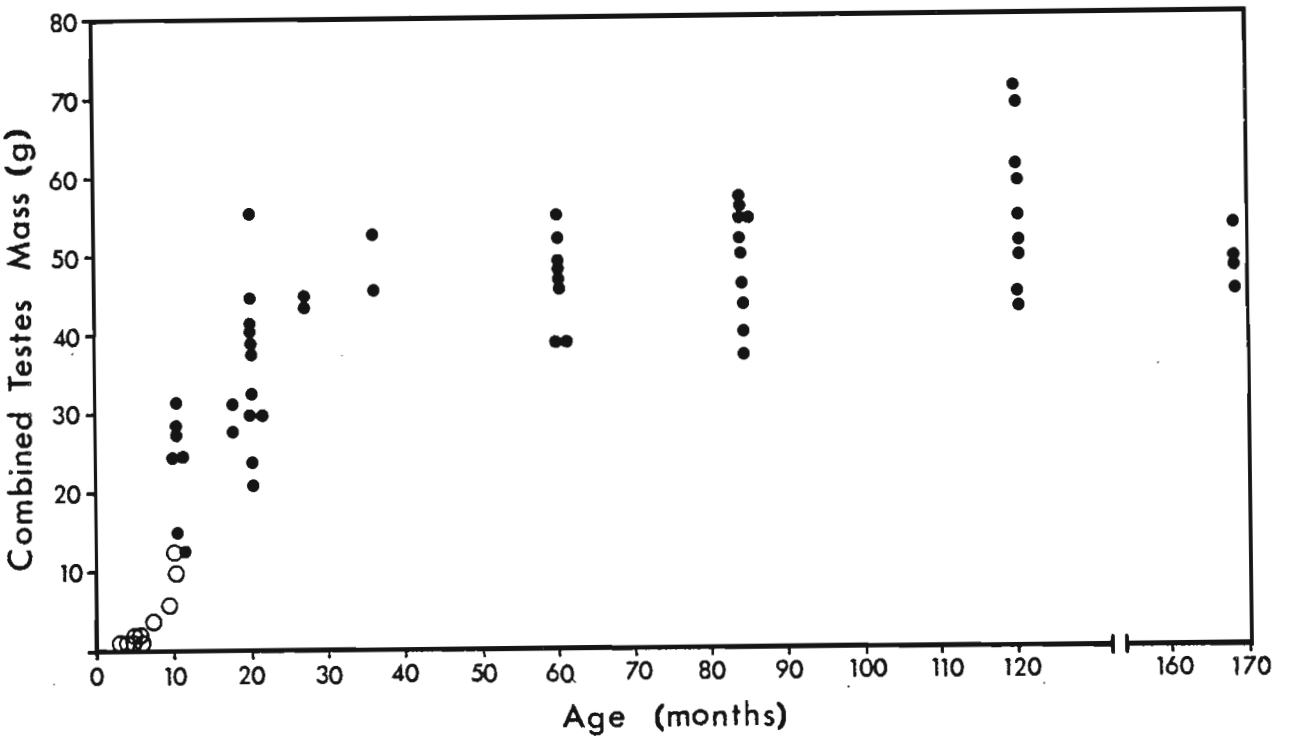


FIGURE 5.8 Growth in mass of testes in duiker with age (open circle - no spermatogenesis; closed circle - at least some through to full spermatogenesis).

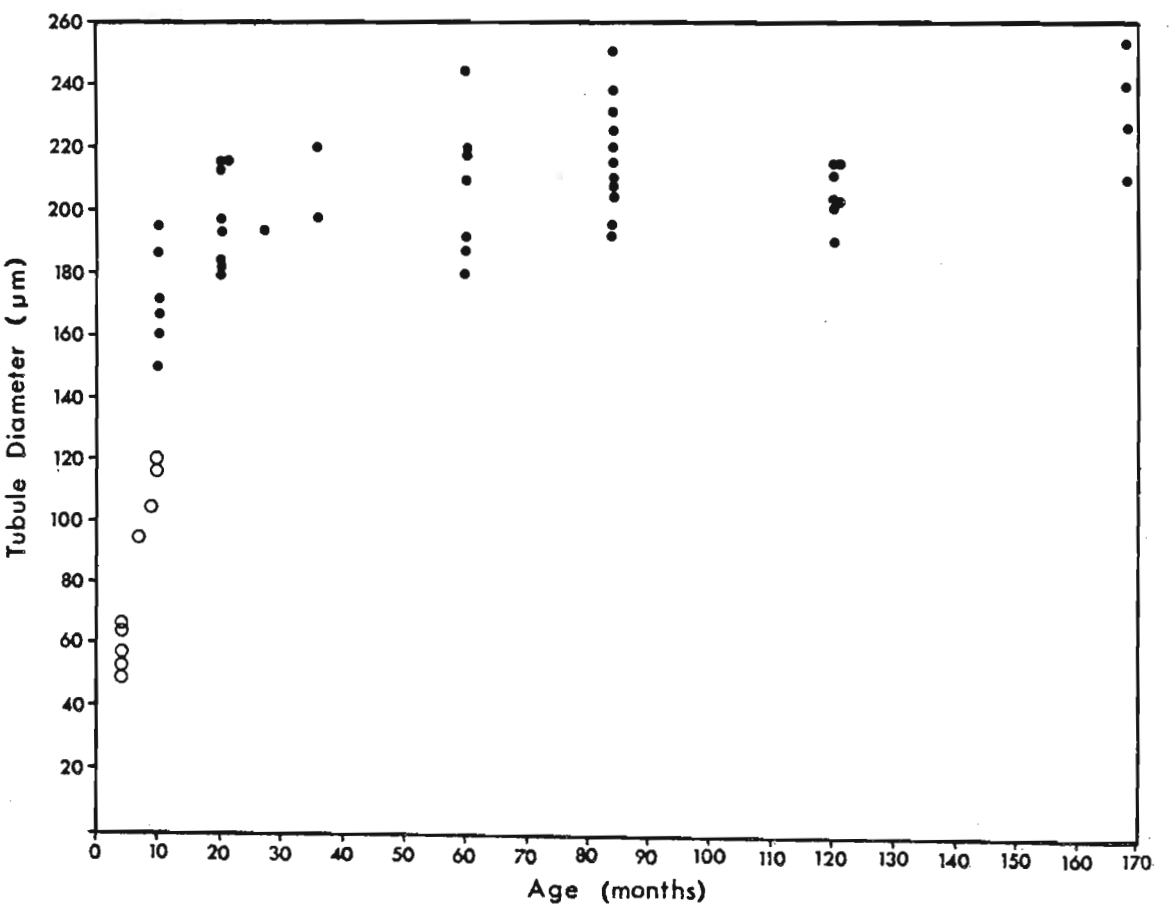


FIGURE 5.9 Variation in mean seminiferous tubule diameter of duiker with age (open circle - no spermatogenesis; closed circle - at least some through to full spermatogenesis).

There was a highly significant relationship between combined testes mass and body mass in prepubertal and postpubertal males (Fig. 5.10). In both prepubertal and postpubertal males, the correlation between combined testes mass and seminiferous tubule diameter (Fig. 5.11) was also highly significant but demonstrated that there can be a considerable reduction in testes mass with little or no change in tubule diameter.

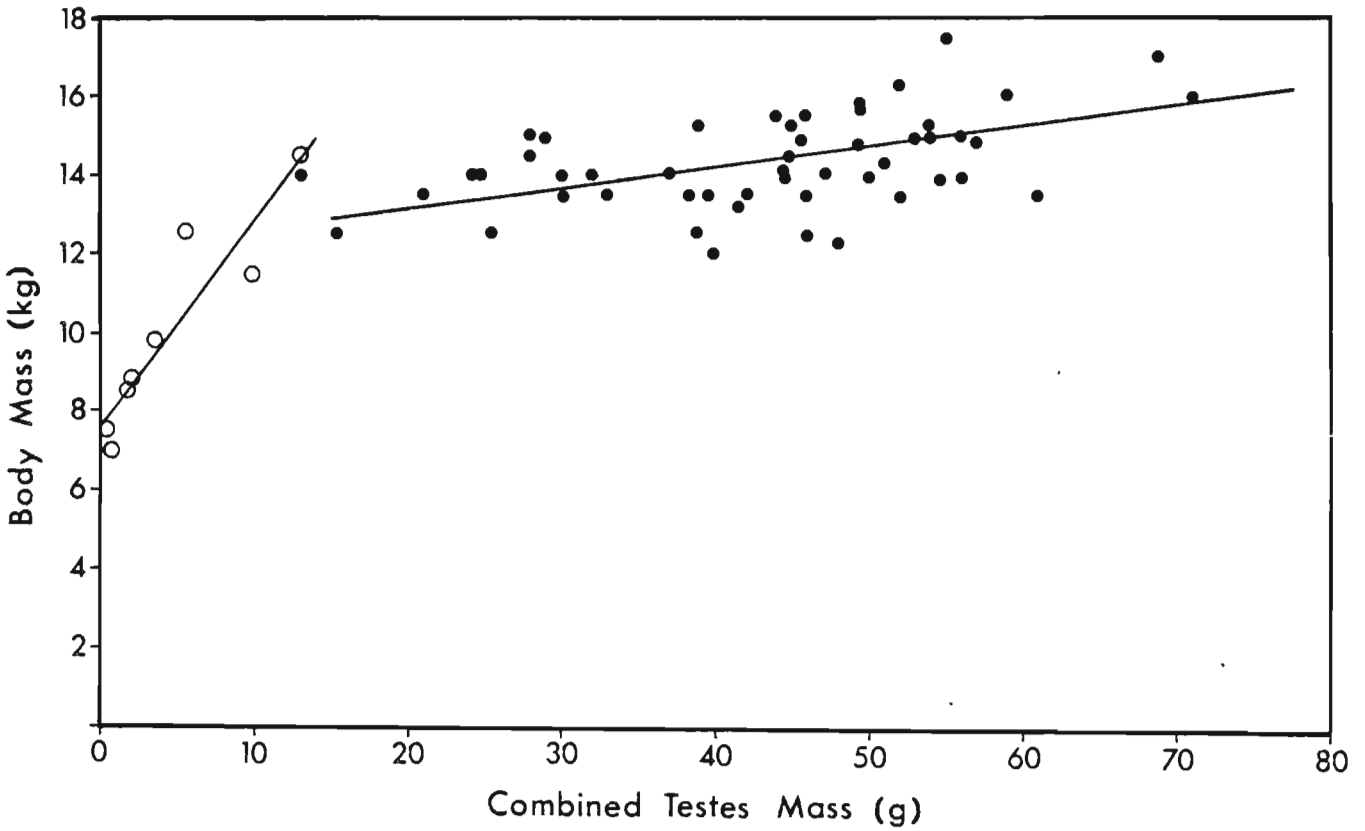


FIGURE 5.10 The relationship between combined testes mass and body mass in duiker. Prepubertal males (open circles) : $y = 0,53x + 7,52$ ($r = 0,925$; $p<0,001$). Postpubertal males (closed circles) : $y = 0,04x + 12,41$ ($r = 0,474$; $p<0,001$).

5.3.2.3 Seasonal changes in the reproductive organs

In order to prevent any bias from young animals that were still growing, only samples from males at least 20 months of age were included in seasonal analyses. Adult testes were largest during the summer months (Fig. 5.12) and were significantly larger than those collected during spring ($t = 2,13$; $p<0,05$). Epididymides mass showed an identical

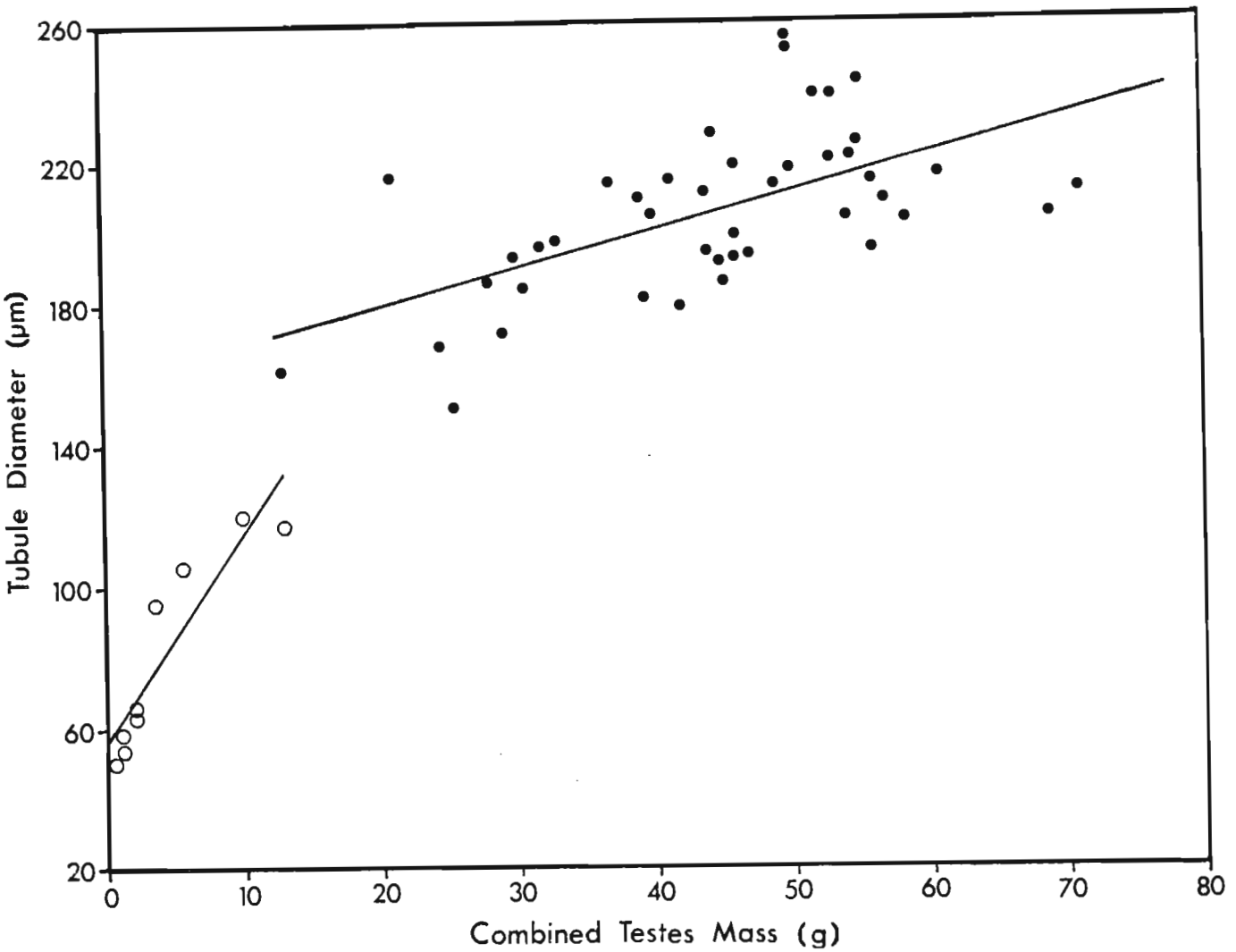


FIGURE 5.11 The relationship between testes mass and seminiferous tubule diameter in duiker. Prepubertal males (open circles) : $y = 5,81x + 56,32$ ($r = 0,918$; $p<0,001$). Postpubertal males (closed circles) : $y = 1,05x + 158,37$ ($r = 0,570$; $p<0,001$).

trend (Table 5.6) where samples from summer were significantly heavier than those from spring ($t = 2,69$; $p<0,02$) while differences in testes and epididymides mass between all other successive seasons were insignificant. Seasonal variation in seminiferous tubule diameter (Table 5.6) was only significant between summer (when tubules were larger) and autumn months ($t = 2,65$; $p<0,02$).

5.3.2.4 Senescence

The presence of spermatozoa in the sections and smears prepared from the epididymides of all males older than 10

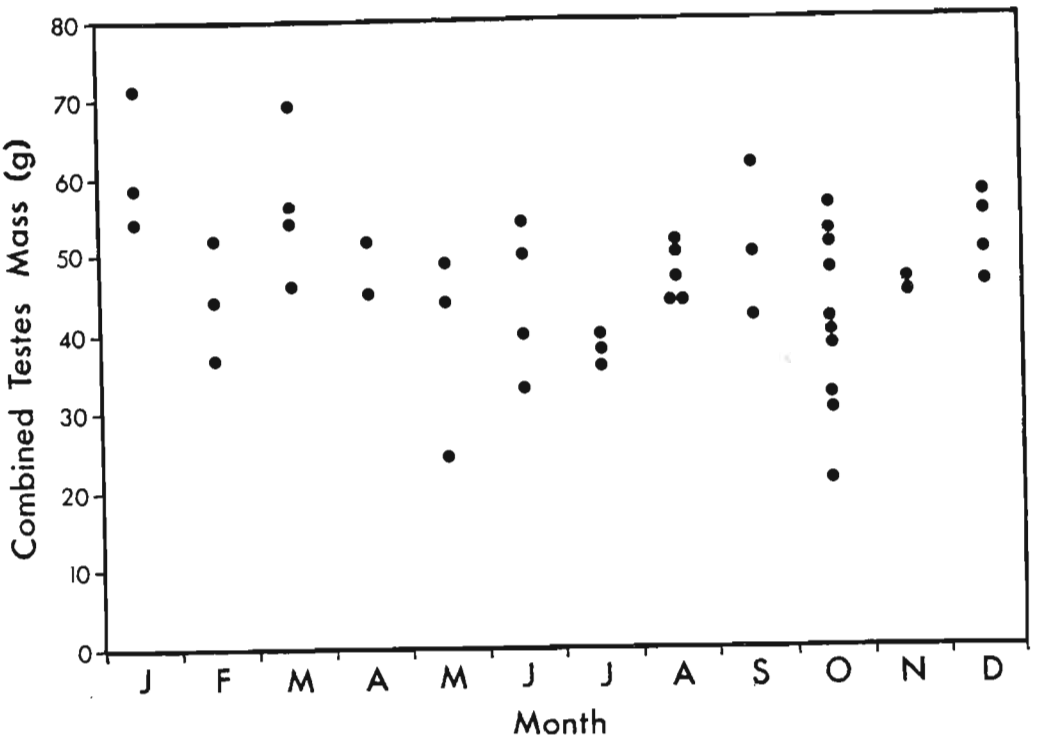


FIGURE 5.12 Monthly variation in combined testes mass of male duiker.

TABLE 5.6 Seasonal variation in testes mass, edididymides mass and seminiferous tubule diameter of male adult duiker. (Mean values are shown + 1 standard error).

Season	Testes mass	Epididymides mass	Seminiferous tubule diam.
Summer (DJF)	52,51±2,90 (n = 10)	9,18±0,30 (n = 10)	219,52±4,72 (n = 11)
Autumn (MAM)	48,86±3,98 (n = 9)	8,84±0,60 (n = 9)	201,65±3,98 (n = 7)
Winter (JJA)	44,59±1,82 (n = 12)	7,68±0,31 (n = 12)	206,07±9,20) (n = 7)
Spring (SON)	43,73±2,76 (n = 15)	7,18±0,57 (n = 15)	210,19±5,18 (n = 15)
All year	46,87±1,47 (n = 46)	8,07±0,27 (n = 46)	210,54±2,98 (n = 40)

months indicated that none of the adult duiker examined were senescent. In fact, reproductive activity as measured by testes and epididymides mass and seminiferous tubule diameters, was greatest in the oldest males of 156-168 months of age.

5.3.2.5 Sexually abnormal males

Unlike bushbuck, five of the male duiker examined had highly disparate left and right testes and epididymides mass (Table 5.7). In two of these (duikers 27 and 61) the smaller of the two testes had not descended into the scrotum and was underdeveloped and sexually inactive. Spermatogenesis was evident in the larger testis of both males, but in duiker 61, spermatozoa were confined to a small section of the sectioned epididymis. No trace of the right testis and epididymis could be found in duiker 11, but active spermatogenesis was found in the left testis. The right testis of duiker 45 had atrophied and was surrounded by a normal sized epididymis containing no spermatozoa, although spermatogenesis was evident in the left testis. The cause of these abnormalities was not determined. In duiker 107, the left testis and epididymis was ascrotal, yet remained attached to the vas deferens and spermatic cord. No histological samples were taken from this testis as it was partially decomposed, but it

TABLE 5.7 Abnormal reproductive tracts of five male duiker.

No.	Age (mth)	Body mass (kg)	Testes mass (g)			Epididymides (g)			Sperm evident in larger testis
			Left	Right	Total	Left	Right	Total	
11	120	14,0	34,24	0,00	34,24	4,44	0,00	4,44	Yes
27	27	13,0	5,63	25,35	30,98	1,58	3,88	5,46	Yes
45	84	15,0	31,12	0,75	31,87	6,84	4,66	11,50	Yes
61	20	14,5	28,44	5,12	33,56	4,79	1,87	6,66	Yes
107	60	10,8	N/R*	20,77	N/R*	N/R*	3,56	N/R*	Yes

* N/R - indicates not recorded

is likely that separation from the scrotum was caused by some form of injury, and that the torn scrotum had healed over, excluding the left testis. Normal activity was recorded from the right testis.

Although none of these duiker were infertile, the tubule diameters of the younger males were lower than the average for their respective age classes. Consequently, and because of the anomalous mass of testes and epididymides, none of these five males were included in any of the analyses detailed above.

5.3.3 Female Bushbuck

5.3.3.1 Puberty and sexual maturity

The ovaries of one (25%) of the 14 month old females contained a corpus luteum, while one of the two 19 month old females and two of the four 21 month old females examined were pregnant. All older bushbuck were reproductively active. Taking puberty as the earliest age at which 50% of the animals in that age class are fertile, puberty occurred at 19 months of age. Three pubertal or postpubertal females had above average body mass when compared to other individuals in their respective age classes (Fig. 5.13): the body mass of the 19 month old pregnant female was not recorded as its carcass had been badly damaged in a road accident. The 14 month old female that had recently ovulated weighed slightly less than one of the immature 21 month old bushbuck, and both were collected on the same day and had almost identical kidney fat indices.

The earliest age at which conception occurred was determined by subtraction of the foetal age from the age of the nulliparous mother, and was found to be 14 months. The mean age at first conception determined from all pregnant, dentally immature females was slightly later at 17,5 months. Assuming a gestation period of 180 days, these females would have given birth for the first time at an average age of 23,5

months. However, the non-pregnant 19 month and 21 month old females would have become primiparous when appreciably older.

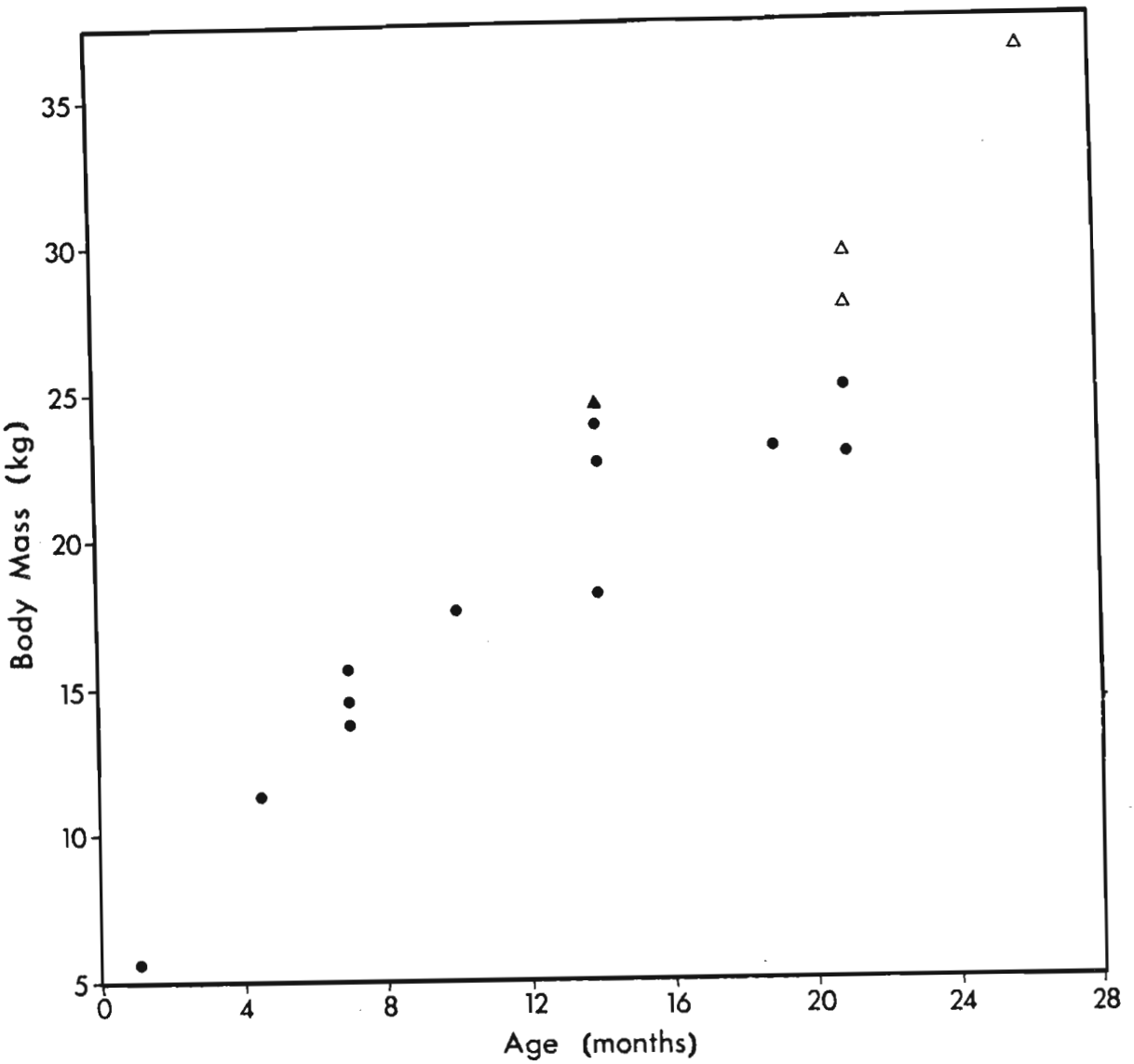


FIGURE 5.13 The relationship between body mass and reproductive status in nulliparous female bushbuck (closed circle - prepubertal female; closed triangle - pubertal female with corpus luteum; open triangle - pregnant female).

5.3.3.2 Ovulation and implantation

The relationship between ovary mass and reproductive status is shown on a monthly basis in Fig. 5.14. The mean mass (± 1 S.E.) of the heaviest ovaries taken from 33 pregnant and non-lactating females was 0,83±0,04g. Pregnant and lactating females (n = 17) had an identical mean heaviest ovary mass of 0,83±0,05g, while nine non-pregnant but lactating females had a mean ovary mass of 0,60±0,08g. The only adult female that was neither visibly pregnant nor

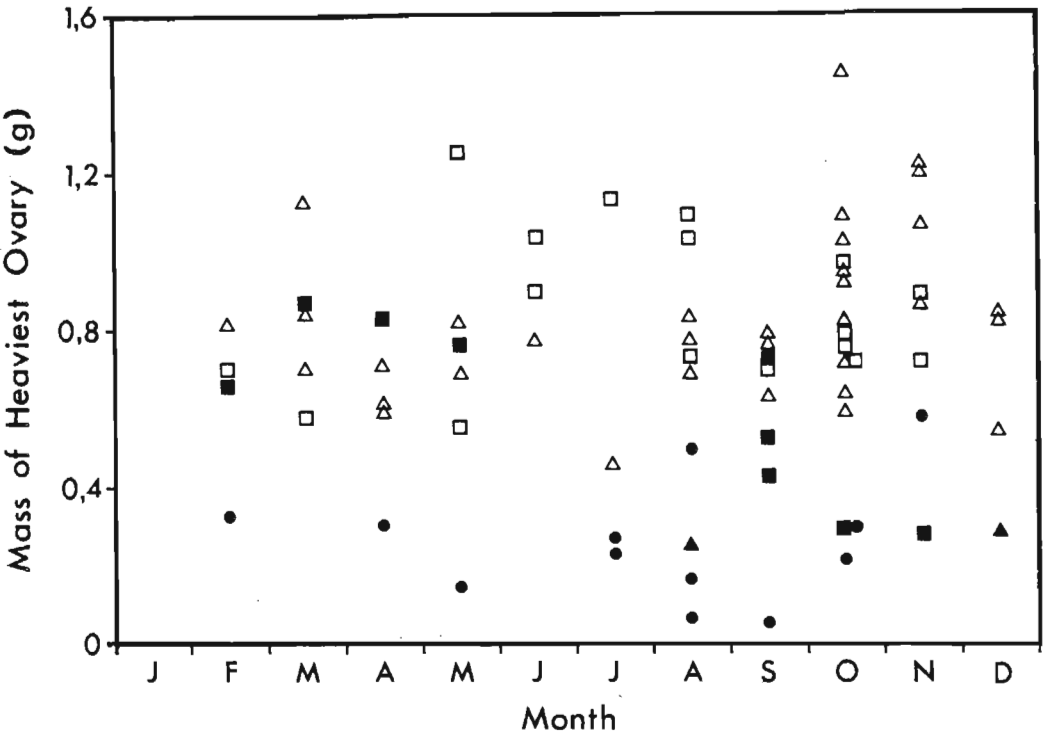


FIGURE 5.14 Monthly variation in heaviest ovary mass in relation to reproductive status of female bushbuck (open square - pregnant and lactating; open triangle - pregnant, non-lactating; closed square - lactating, non-pregnant; closed triangle - not visibly pregnant but with corpus luteum; closed circle - non-pregnant, non-lactating).

lactating had a corpus luteum in both the left and right ovaries which weighed 0,29 and 0,26g respectively, and the left ovary of a 14 month old female contained a corpus luteum and had a mass of 0,25g. The mean mass of the heaviest ovaries collected from 12 prepubertal females weighed slightly more at 0,27±0,05g. No meaningful relationships were evident between heaviest ovary (containing a corpus luteum) and duration of pregnancy for either pregnant or pregnant and lactating parous females (Fig. 5.15).

Although ovulation occurred most frequently (63%) in the right ovary, the difference in the rate of ovulation between left and right ovaries was not significant. Implantation was also more common (63%) in the right uterine horn, and occurred on the same side as ovulation in 86% of the 52 examined pregnancies. Contralateral implantations resulted from both left and right ovulations.

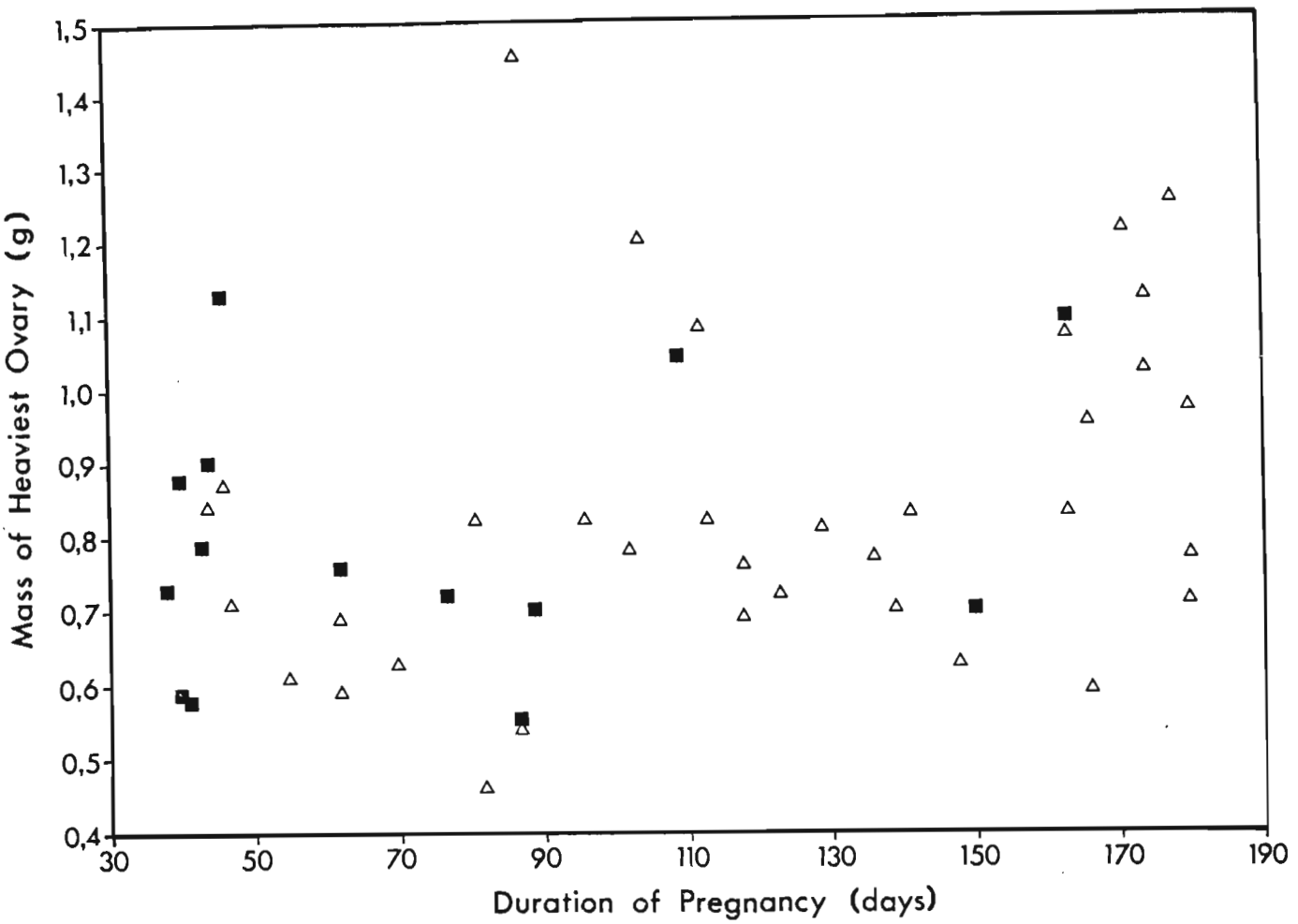


FIGURE 5.15 Changes in the mass of the heaviest ovary (containing a corpus luteum) of bushbuck during pregnancy (open triangle - pregnant female; closed square - pregnant and lactating female).

In addition to the multiple ovulation of the non-pregnant and non-lactating adult female mentioned above, a 72 month old female was collected with dizygotic twin foetuses. Both twins were female, and ovulation had occurred from both left and right ovaries, with subsequent implantation in both left and right uterine horns.

5.3.3.3 Fertility, conception rates and parturition intervals

The presence of a corpus luteum, an embryo or foetus, and/or milk in the udder was regarded as positive evidence of fertility. Table 5.8 reveals that 66 of the 78 females examined were reproductively active (i.e. a crude conception

TABLE 5.8 The breeding status of 78 female bushbuck in relation to age.

Reproductive Status	Age Class (Months)										
	1-10	14	19	21	26	48	72	96	132	156	Total
Sample Size	6	4	2	4	1	10	18	19	13	1	78
Not pregnant, non-lactating and without corpus luteum	6	3	1	2	0	0	0	0	0	0	12
(% of age class)	(100%	(75%)	(50%)	(50%)	-	-	-	-	-	-	
Not visibly pregnant, non-lactating but with corpus luteum	0	1	0	0	0	1	0	0	0	0	2
(% of age class)	-	(25%)	-	-	-	(10%)	-	-	-	-	
Pregnant, non-lactating	0	0	1	2	1	4	11	9	7	1	36
(% of age class)	-	-	(50%)	(50%)	(100%)	(40%)	(61%)	(47%)	(54%)	(100%)	
Pregnant and lactating	0	0	0	0	0	3	6	5	3	0	17
(% of age class)	-	-	-	-	-	(30%)	(33%)	(26%)	(23%)	-	
Lactating, not pregnant	0	0	0	0	0	2	1	5	3	0	11
(% of age class)	-	-	-	-	-	(20%)	(6%)	(26%)	(23%)	-	
Number Breeding	0	1	1	2	1	10	18	19	13	1	66
(% of age class)	-	(25%)	(50%)	(50%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	

rate of 85%) and that all females older than 21 months were fertile. Of these 62 postpubertal animals, 50 (81%) were pregnant or pregnant and lactating, while 28 (45%) were lactating or lactating and pregnant. Specific conception rates of 100% were therefore attained throughout life, and there was no evidence of sexual senescence in this population.

The mean lambing interval was calculated from the formula of Short (1966) which has been used in numerous subsequent reproductive studies (e.g. Anderson 1978; Hanks 1979; Spinage 1982), where:

$$\frac{\text{Interval between pregnancies(I)}}{\text{Gestation period}} = \frac{\text{Number of non-pregnant females}}{\text{Number of pregnant females}}$$

Thus for postpubertal bushbuck;

$$I = \frac{11}{51} \times 180 = 39 \text{ days}$$

This interval between pregnancies, added to the gestation period, provided a mean parturition interval of 219 days, or approximately 7,5 months.

Parturition intervals were also calculated from pregnant females that were culled together with their infants. Seven adult females were shot with an accompanying offspring, the youngest of which was estimated by tooth eruption patterns to be a suckling 4,5 months old. The mother had a 77 day old foetus, and therefore conceived approximately 60 days post-partum. The lambing interval in this instance was therefore approximately 8 months. Two other females were culled together with their 7 month old offspring and both adults had foetuses of just under 3 months of age. These two bushbuck therefore conceived approximately 4 months after parturition, and had lambing intervals of approximately 10 months. The ages of the other four bushbuck culled with

their mothers were too advanced to permit estimation of parturition intervals in this manner.

5.3.3.4 Lactation

The mean udder mass of 23 pregnant but not lactating parous adults was 52,1g (±2,9g S.E.). Udders from 18 lactating parous females were on average five times heavier, with a mean mass of 290,9g ± 31,6g. Six glands secreting colostrum had a mean mass of 174,4g ±49,4g; these were classified as pregnant rather than pregnant and lactating in all subsequent analyses. The mammary glands from eight immature females had a mean mass of 11,7g ±1,9g. Changes in mammary gland mass during pregnancy are shown in Fig. 5.16, and indicate that lactation may persist for up to 3,5 months after conception, while colostrum is produced during the last 10 days of pregnancy. Assuming a mean interval between pregnancies of 39 days, these data suggest that females lactate for up to 5 months after parturition. Evidence from females culled together with their infants generally support this conclusion. One adult female shot with her 4,5 month old infant was still lactating and had a 77 day old foetus. Another adult, with a foetus of 82 days, was not lactating when culled with her 7 month old juvenile. However, a third female, also pregnant with an 87 day old foetus, was still lactating when shot with her 7 month old offspring, thereby suggesting that lactation may, in some instances, last for at least 7 to 8 months.

5.3.3.5 Foetal sex ratio

A total of 55 females were visibly pregnant, but only 45 embryos and foetuses were sufficiently developed for the identification of sex. Of these, 25 were males and 20 were females (125 males:100 females). This ratio does not significantly differ from parity.

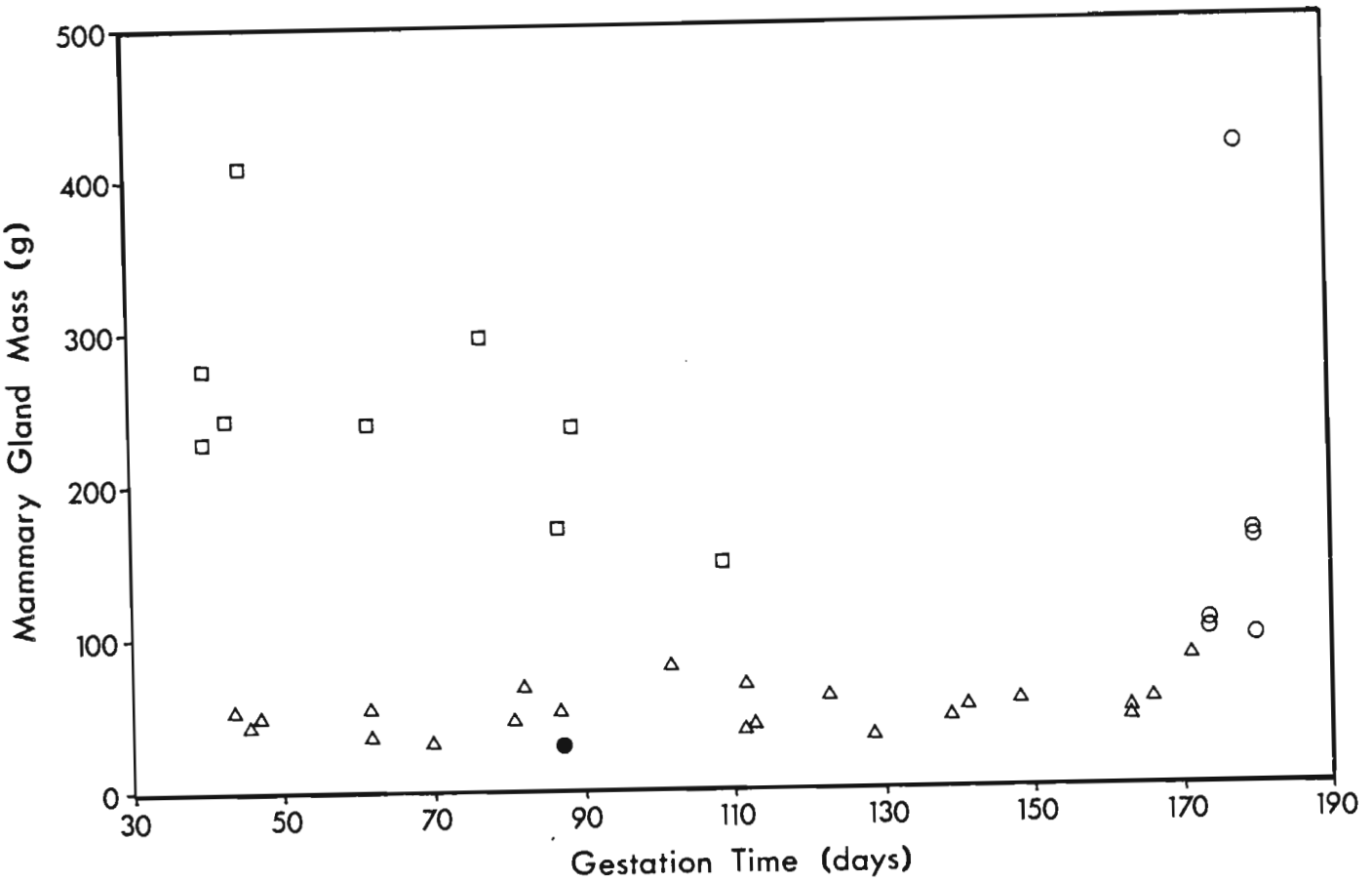


FIGURE 5.16 Variation in mammary gland mass with duration of pregnancy in female bushbuck (open square - lactating and parous; open triangle - non-lactating, parous; open circle - gland secreting colostrum; closed circle - non-lactating, nulliparous).

5.3.3.6 Seasonality of conceptions and births

Foetal ages were determined by the Huggett and Widdas (1951) equation, using a birth mass of 3 400g and a mean gestation period of 180 days to determine the specific growth velocity, "a". Since the subspecies in this study was found to be considerably larger than the other subspecies studied elsewhere (Chapter Three), it is probable that the average mass of newborn bushbuck would also be greater in T.s.sylvaticus, and in fact three of the full term foetuses measured from Weza exceeded 3 400g. However, substituting a birth mass of 4 000g (the mass of the heaviest foetus from this study) into the Huggett and Widdas equation delayed the estimated conception date of a 100 day old foetus (determined from a birth mass of 3 400g) by only three days, and since most previous studies of seasonal breeding in this species

have employed a birth mass and gestation period of 3 400g and 180 days respectively, these values were utilized for comparative purposes in this study. Birth dates and conception dates were determined by extrapolation of foetal age, and for the three foetuses heavier than the average birth mass, predicted parturition dates exceeded the average length of gestation by one to eight days.

Parturition dates were calculated for all pregnant females collected during the period from September 1980 to May 1984 and are illustrated at monthly intervals in Fig. 5.17 which also shows the number of postpubertal females examined each month during this period. There was no evidence of seasonality from the data obtained in 1980 and up to mid-1981, but thereafter birth peaks in late winter, spring and early summer were apparent in all subsequent years. These closely followed the unequal distribution of culled mature females however (Fig. 5.17) and date of birth was found to be highly correlated to date of collection ($r = 0,871$; $p<0,001$). In fact, 63% of all births occurred during the months of August to December (Fig. 5.18), when 66% of all postpubertal females were collected (Fig. 5.19). It is therefore highly probable that unequal sampling intensities would influence conclusions regarding reproductive seasonality, particularly since conception rates exceeded 80% throughout the course of this study. Several authors have attempted to remove sampling bias by considering the "possible" or "potential" number of conceptions or birth each month in relation to gestation length (e.g. Anderson 1978; Howard 1983), but since the duration of gestation in the bushbuck is only six months, such efforts could only reduce, but not remove, all sources of sampling bias for this species over a twelve month period.

An alternative method, employed in this study, involved comparisons of the pregnancy rates of females at different times of the year, using the "d" test of Bailey (1959). Pregnancy rates could not be compared meaningfully between individual months because of the vastly different sample sizes of postpubertal females (Fig. 5.20). In every

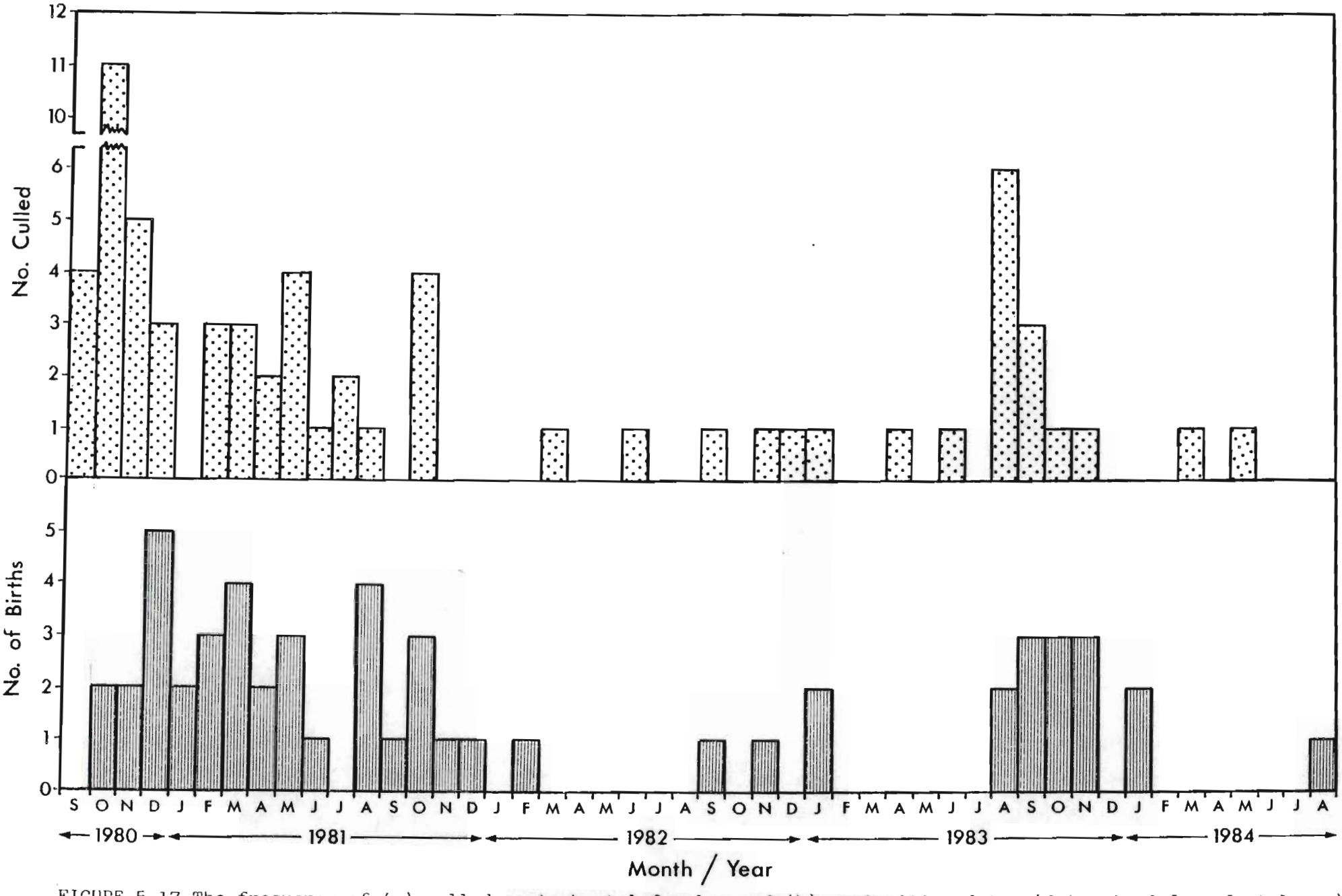


FIGURE 5.17 The frequency of (a) culled postpubertal females and (b) parturition dates (determined from foetal age) of bushbuck from the period September 1980 to August 1984.

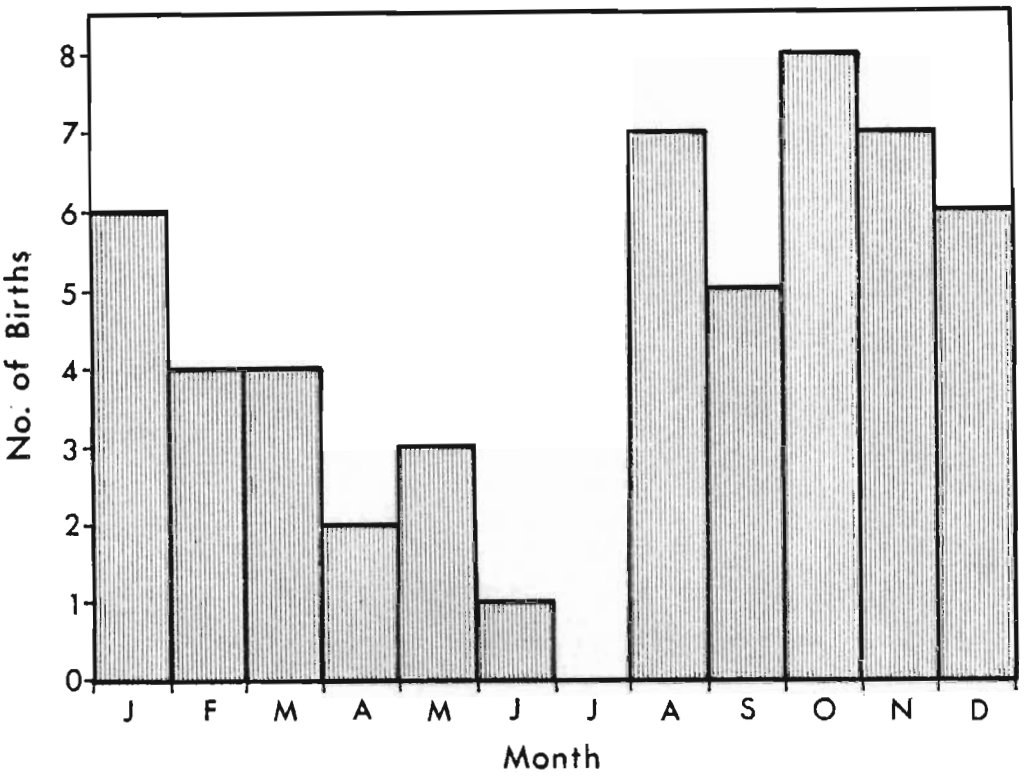


FIGURE 5.18 Accumulated parturition dates of bushbuck determined from foetal age.

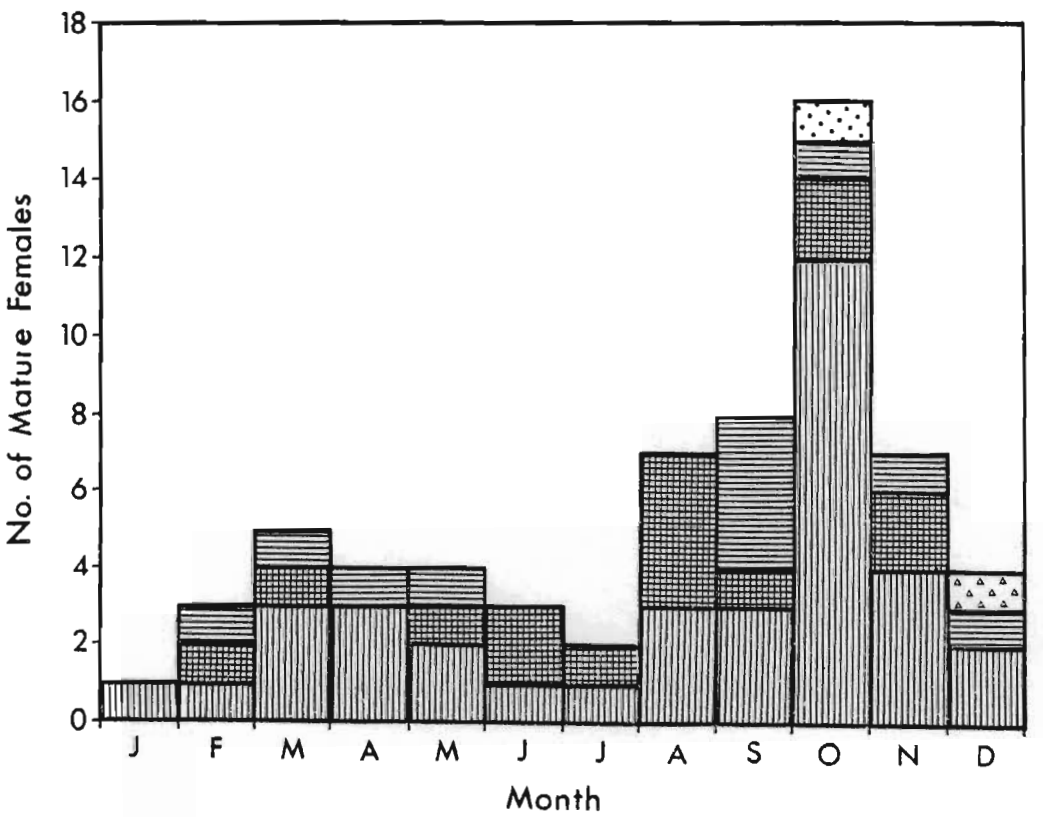


FIGURE 5.19 Variation in the number and reproductive status of mature female bushbuck examined each month. (= pregnant; = pregnant and lactating; = lactating; = not pregnant, not lactating; = status unknown).

instance, the proportions of pregnant females collected during one season did not differ significantly from those of the succeeding season. Further, the pregnancy rate of females examined in January to June (80%) was almost identical to the rate determined from females in the second half of the year (81%). Similar tests were not performed on the proportions of adult females lactating each season (as shown in Fig. 5.20) since the duration of lactation could not be determined as accurately as for gestation, and would further be influenced by neonatal and infant mortality as well as subsequent reproductive performance.

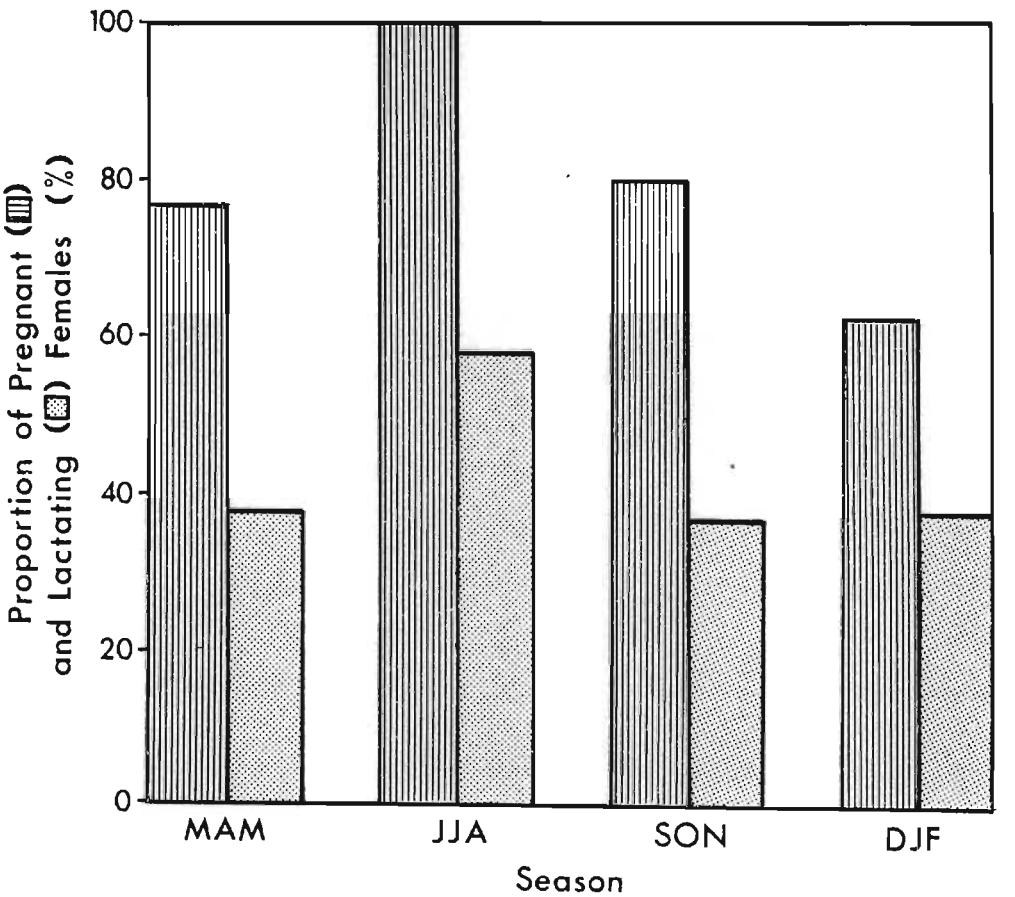


FIGURE 5.20 Seasonal changes in the proportions of pregnant and lactating female bushbuck.

Birth dates were also determined by subtraction of the age of each subadult from the date it was collected. Although the 34 births determined by this means occurred throughout the year, 67% of the subadults were born during July to December (Fig. 5.21). Of the five subadults breeding

for the first time, two had been born in winter and one in each of the other three seasons. There was no obvious trend in the times at which they became sexually mature (February, March, July and September) when compared to the conception dates of older females (as determined from foetal ages, Fig. 5.22).

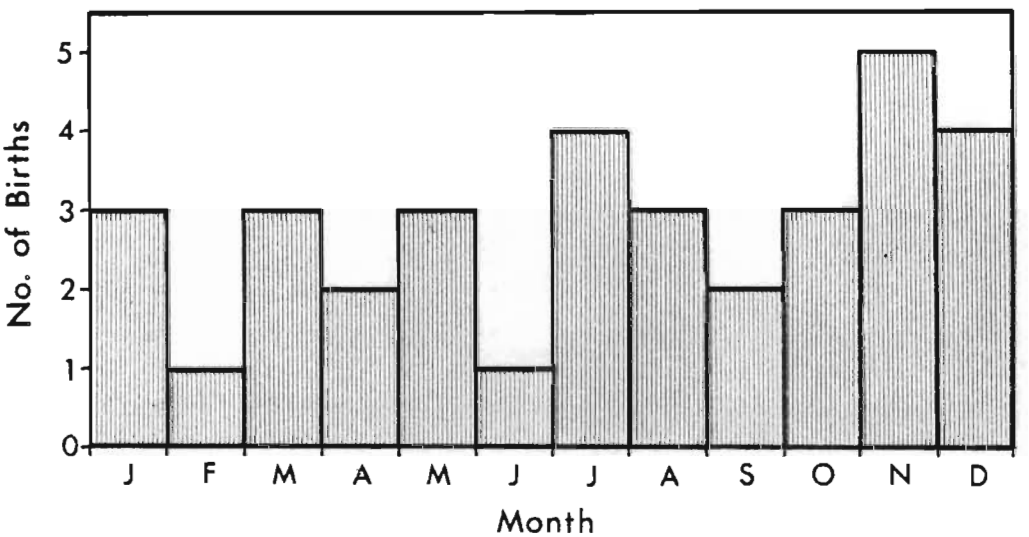


FIGURE 5.21 Birth dates of bushbuck determined by back-dating the estimated ages of infants and juveniles.

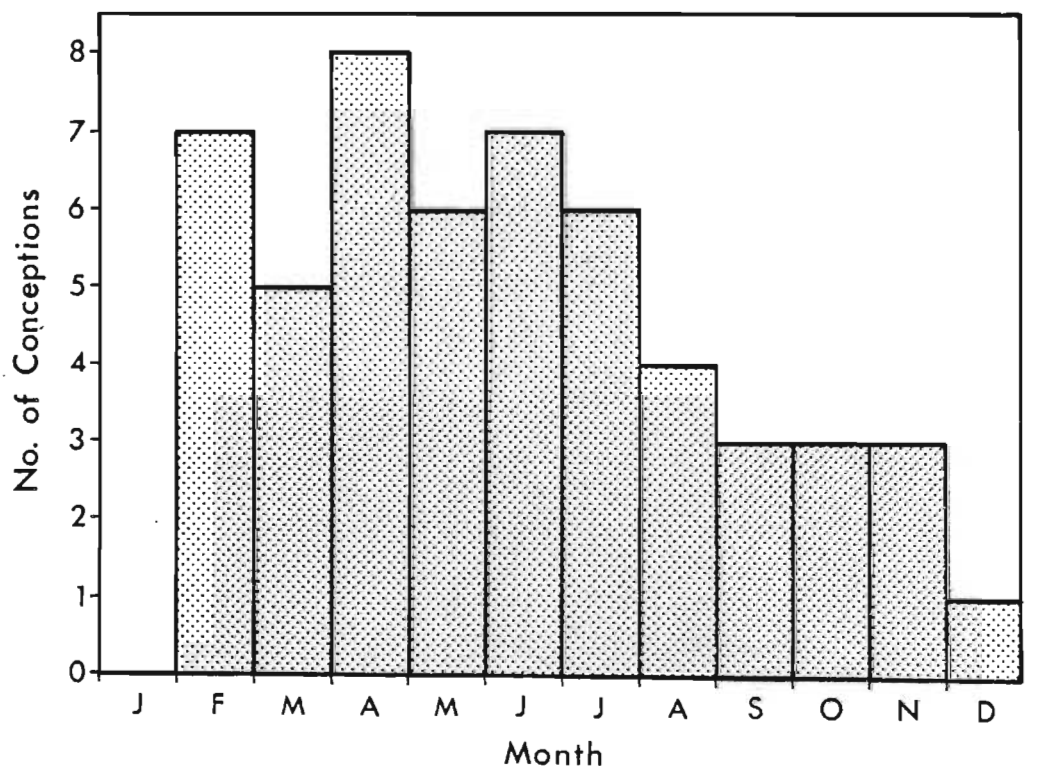
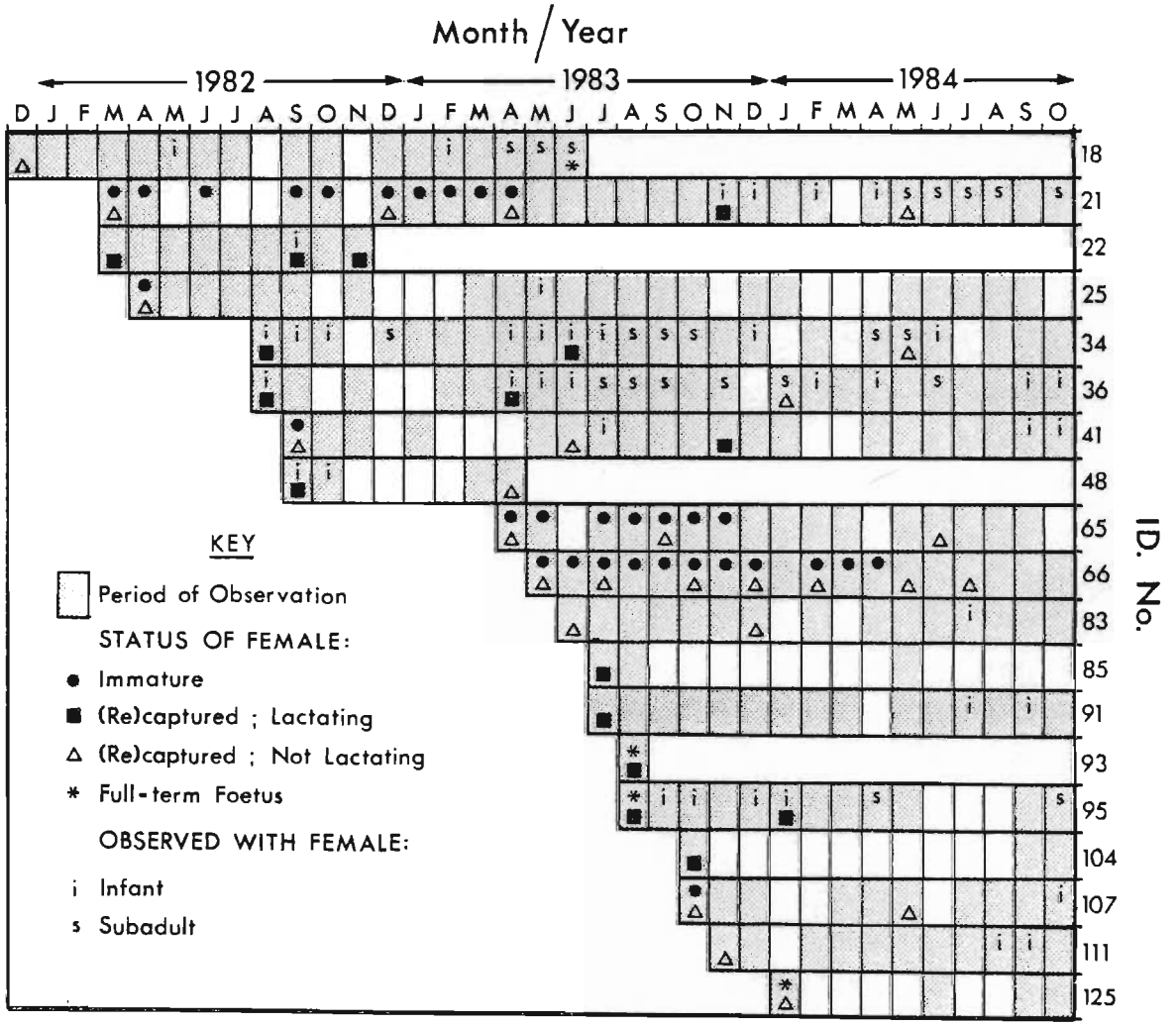


FIGURE 5.22 Accumulated conception dates of bushbuck determined from foetal age.

5.3.3.7 Field Observations

The ages at which females became primiparous were estimated from regular sightings of four marked females. One of these, No. 41 in Table 5.9, was recaptured the month before she was seen with her infant, and was not lactating. From these observations it was concluded that this female, which was estimated to be 21 months old when initially captured 10 months previously, gave birth for the first time at the age of 31 months. The age at first parturition of the other three marked females could not be assessed with the same degree of accuracy. Two of these, bushbuck 107 and 21, had immature udders when recaptured five and seven months prior to their observed associations with infants, when their ages were estimated at 28 and 21 months respectively.

TABLE 5.9 The reproductive histories of 19 captured, marked and released female bushbuck.



Parturition had therefore occurred by the time bushbuck 107 was 33 months old. Bushbuck 21 was recaptured again during the month she was first seen with an infant, and was lactating at this time when she was estimated to be 28 months of age. The fourth marked female (bushbuck 25, Table 5.9) was captured when 21 months old, and although not recaptured, was seen regularly on her own for the next twelve months, but only with an infant when 34 months old.

Two additional females were marked when juveniles of 10 months and 14 months of age. The younger animal, bushbuck 66 (Table 5.9) was immobilized and examined on seven occasions, but still had an underdeveloped udder when recaptured for the last time at 24 months old. Bushbuck 65 was recaptured twice, but still had an immature udder when 29 months old. Neither of these females had been seen with an infant at foot when field work was terminated several months later, and since these bushbuck had been examined or observed almost every month (Table 5.9) it is highly probable that neither had lambed by the age of 27 months (bushbuck 66) or 31 months (bushbuck 65).

Records of the shortest periods of time when marked females were observed with successive infants provided another means of determining parturition intervals. Table 5.9 shows that four females (bushbuck 18, 34, 36 and 41) produced a total of 13 infants during the study period, at an average interval of 8,1 $\pm$ 0,9 months. Concealment and lying-out behaviour of neonates, and the unequal distribution of bushbuck sightings during the year may have resulted in an overestimation of lambing intervals however, particularly since lying-out behaviour varied considerably between individuals. Bushbuck 18 was first seen with her second recorded infant in February 1983, and died with a full term foetus in mid June of the same year (Table 5.9), suggesting that the infant was at least 2,5 months old when first observed. In contrast, when bushbuck 95 was captured in August, she was heavily pregnant and producing colostrum. This animal was seen with a neonate eight days later and the infant and mother were observed a further four times during

that month, once together in October, and three times in December.

Thirty-three females were examined while immobilized and of these, 16 (48%) were lactating and four, which were caught in January, June and August, had full term foetuses. The duration of lactation could rarely be assessed from recaptured animals since the precise breeding status of marked females could not always be determined and was restricted to superficial examinations at irregular intervals of capture. For example, bushbuck 34 and bushbuck 36 were both lactating when captured and were also lactating nine and eight months later respectively, at which time they were probably nursing new infants (Table 5.9). Bushbuck 22 was lactating when captured in March, and again in September when she had an attending infant. This animal was killed by dogs in November, and although not pregnant, was still producing milk, presumably for her second infant seen in September (Table 5.9). The only animal to provide a minimum period of lactation was bushbuck 95, which was heavily pregnant and producing colostrum when initially captured, and was regularly seen with her infant until recapture five months later, at which time she was still nursing.

Capture and recapture operations were most successful during the winter months (see Appendix D) and marked animals therefore provided limited data regarding reproductive seasonality. In addition, courtship behaviour was observed too infrequently (on five occasions) to provide any indication of seasonal breeding. This aspect was evaluated from sightings of infant bushbuck recorded during routine field work in the first year of study (when duplicated observations were less likely, see Chapter Nine). The proportions of infants, expressed as a percentage of the total number of bushbuck seen each month, was highest in November, but apart from March when no infants were observed, remained relatively constant for the rest of the year (Fig. 5.23).

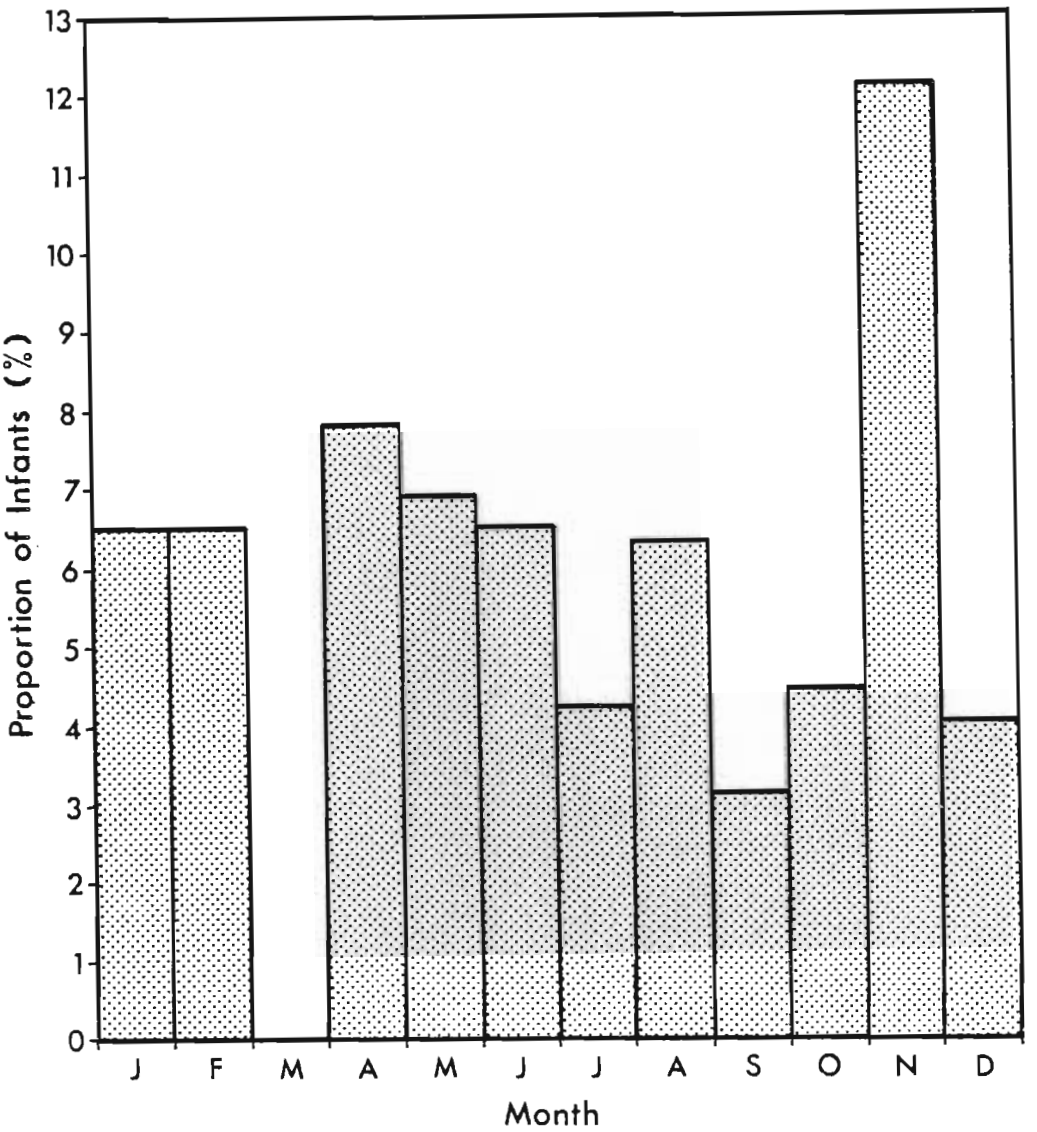


FIGURE 5.23 Sighting frequencies of infant bushbuck between November 1980 and October 1981 expressed as a proportion (%) of all bushbuck seen per month. (Total number of observations = 944).

5.3.4 Female Duiker

5.3.4.1 Puberty and sexual maturity

One of the two 9 month old duiker examined was pregnant, as were three of the eight 10 month old females. Ovulation had recently occurred in another of the 10 month old females. All older females were reproductively active, and puberty was therefore attained at 9 months of age.

The four fertile 10 month old duiker were all heavier than their immature peers, but three of the latter were

heavier than the 9 month old pregnant duiker (Fig. 5.24). All of these animals were collected in spring and summer, when their kidney fat indices differed by less than 2%.

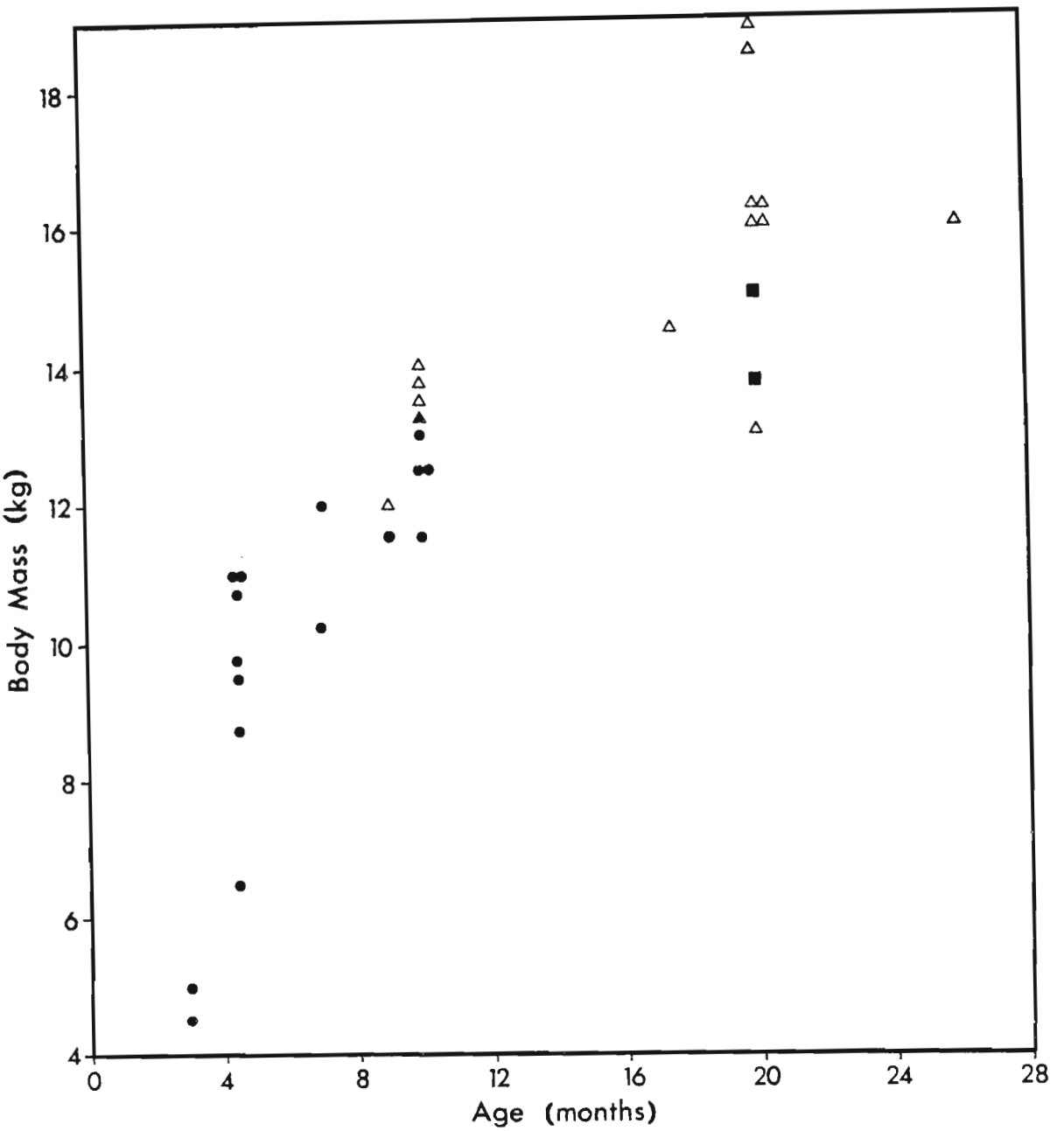


FIGURE 5.24 The relationship between body mass and reproductive status in nulliparous female duiker (closed circle - prepubertal female; closed triangle - pubertal female with corpus luteum; open triangle - pregnant female; closed square - lactating female).

One 10 month old female had an 88 day old foetus and therefore conceived at 7 months of age, and the mean age of first conception, estimated from four nulliparous duiker was

7,5 months. Assuming a gestation period of 191 days, these duiker would have given birth at an average age of 14 months.

5.3.4.2 Ovulation and implantation

Monthly variations in ovary mass related to reproductive conditions are shown in Fig. 5.25. The mean mass (± 1 S.E.) of the heaviest ovaries taken from 24 pregnant and non-lactating female duiker was 0,41 ± 0,02g. The heaviest ovaries taken from nine pregnant and lactating females had a considerably higher mean mass of 0,67 ± 0,16g, and the corresponding value for six non-pregnant but lactating females was 0,61 ± 0,16g. The right ovary from one ten month old female contained a corpus luteum and had a mass of 0,45g,

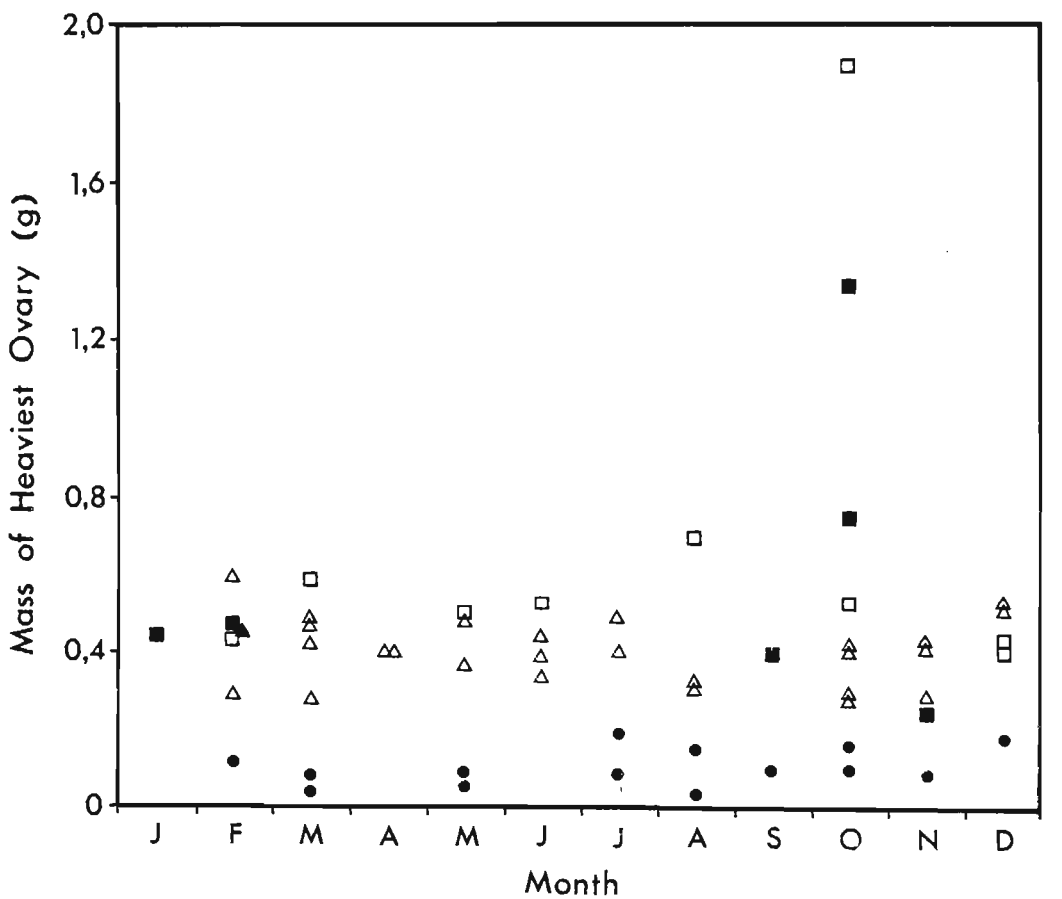


FIGURE 5.25 Monthly variation in heaviest ovary mass in relation to reproductive status of female duiker (open square - pregnant and lactating; open triangle - pregnant, non-lactating; closed square - lactating, non-pregnant; closed triangle - not visibly pregnant but with corpus luteum; closed circle - non-pregnant, non-lactating).

while the heaviest ovaries from one non-pregnant and non-lactating adult and 14 postpubertal females had a mean mass of 0,11 ± 0,01g. There was no obvious relationship between heaviest ovary mass and duration of pregnancy for either pregnant or pregnant and lactating females (Fig. 5.26).

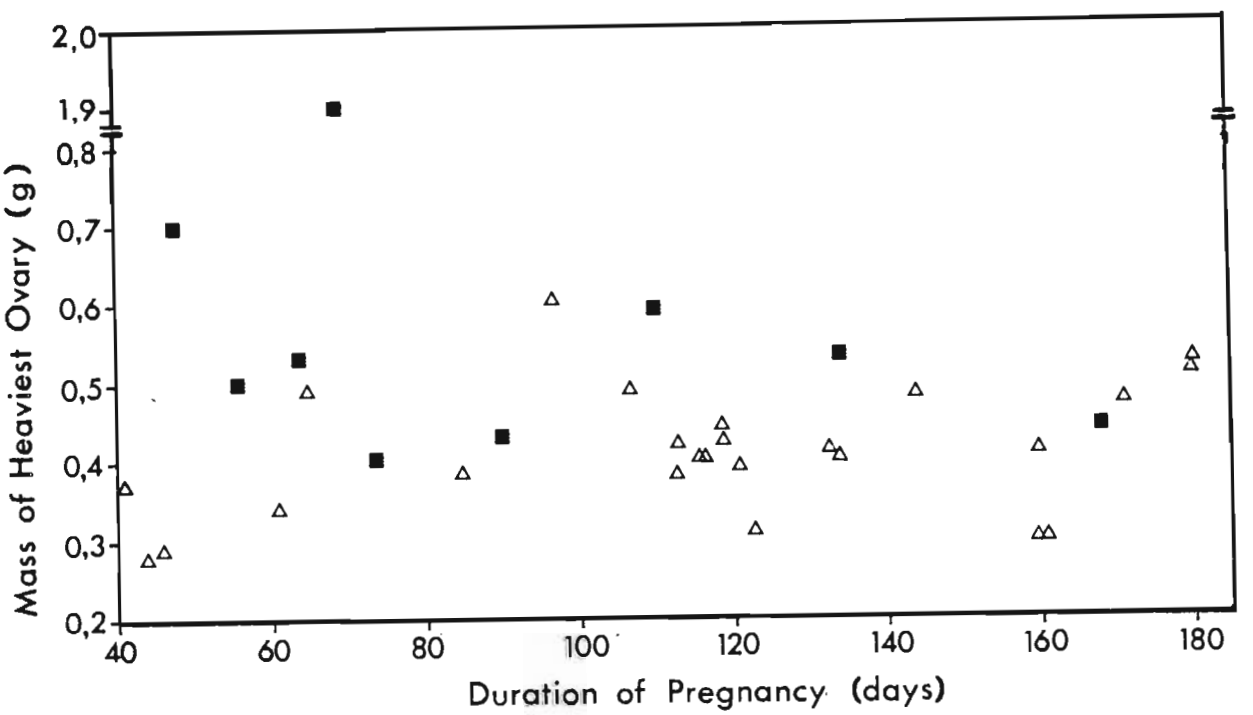


FIGURE 5.26 Changes in the mass of the heaviest ovary (containing a corpus luteum) of duiker during pregnancy (open triangle - pregnant female; closed square - pregnant and lactating female).

Implantation always occurred in the right horn of the uterus, and ovulations were almost equally distributed between left (44%) and right (56%) ovaries. The proportions of contralateral and ipsilateral implantations were therefore 44% and 56% respectively.

5.3.4.3 Fertility, conception rates and parturition intervals

As for bushbuck, the presence of a corpus luteum, an embryo or foetus, and/or milk in the udder was regarded as positive evidence of fertility. Forty-nine of the 69 females examined were reproductively active (i.e. a crude conception

rate of 71%) and all animals over the age of 10 months were fertile with the possible exception of one 120 month old female (Table 5.10). This animal was neither pregnant or lactating, and no corpora lutea or corpora albicantia were detected in her ovaries, which had a similar mass to those of prepubertal duiker. However, it was evident from the size of the uterus and the udder that this adult was parous, and therefore probably fertile. All of the seven older females (168 months old) were actively breeding, and it is therefore unlikely that the 120 month old duiker had become sexually senescent. It is possible that this animal may have lost an infant (and therefore was not lactating) and was culled prior to ovulation.

Of the sample of 45 postpubertal duiker, 84% were pregnant or pregnant and lactating, and 38% were lactating or lactating and pregnant. With the exception of the one 120 month old female, which lowered the fertility of that age class to 87,5%, specific conception rates of 100% were attained through life (Table 5.10).

Using the formula of Short (1966), the mean interval between pregnancies was calculated as follows:

$$\frac{\text{No. non-pregnant adult females(7)}}{\text{No. pregnant adult females(38)}} \times \text{gestation period (191 days)}$$

$$= 35 \text{ days}$$

This interval between pregnancies, combined with the gestation period, yielded a mean parturition interval of 226 days or approximately 7,5 months.

Parturition intervals were also determined from two females that had been culled together with their infants. If the age of 4,5 months estimated by tooth eruption patterns was correct for the younger infant, then the mother, which had a foetus of 134 days, would have conceived within one or two days post-partum. The older offspring was an estimated 7

TABLE 5.10 The breeding status of 69 female duiker in relation to age.

Reproductive Status	Age Class (Months)										
	1-7	9	10	17,5	20	27	60	84	120	168	Total
Sample size	14	2	8	1	9	3	6	11	8	7	69
Not pregnant, non-lactating and without corpus luteum	14	0	4	0	0	0	0	0	1	0	19
(% of age class)	(100%)	-	(50%)	-	-	-	-	-	(12,5%)	-	
Not visibly pregnant, non-lactating but with corpus luteum	0	1	1	0	0	0	0	0	0	0	2
(% of age class)	-	(50%)	(12,5%)	-	-	-	-	-	-	-	
Pregnant, non-lactating	0	1	3	1	6	2	4	7	4	3	31
(% of age class)	-	(50%)	(37,5%)	(100%)	(66,7%)	(66,7%)	(66,7%)	(63,6%)	(50%)	(4,29%)	
Pregnant and lactating	0	0	0	0	1	1	1	2	3	3	11
(% of age class)	-	-	-	-	(11,1%)	(33,3%)	(16,7%)	(18,2%)	(37,5%)	(42,9%)	
Lactating, not pregnant	0	0	0	0	2	0	1	2	0	1	6
(% of age class)	-	-	-	-	(22,2%)	-	(16,7%)	(18,2%)	-	(14,2%)	
Number Breeding	0	1	4	1	9	3	6	11	7	7	49
(% of age class)	-	(50%)	(50%)	(100%)	(100%)	(100%)	(100%)	(100%)	(87,5%)	(100%)	

months of age, and the mother of this juvenile had a foetus of 171 days, indicating an interval between pregnancies of 39 days. The parturition intervals of these two duiker were therefore approximately 6,5 and 7,5 months respectively.

5.3.4.4 Lactation

Twelve non-lactating, pregnant duiker had a mean udder mass of 33,8 ± 3,2g. Udders from 10 lactating, parous females were, on average, more than five times heavier with a mean mass of 191,8g ± 31,8g. Three glands with a mean mass of 179,8g were secreting colostrum, but these females were considered as pregnant females with full-term foetuses rather than pregnant and lactating females in all subsequent classifications. The mammary glands of six pregnant but nulliparous females had a mean mass of 13,5 ± 1,5g, while the mean mass of glands from 10 immature females was 8,7 ± 0,9g. One adult female that was neither pregnant or lactating, but from dimensions of the uterus and udder had given birth to previous young, had an udder mass of 17,8g.

Changes in mammary gland mass during pregnancy are illustrated in Fig. 5.27 and suggest that weaning may occur up to 4,5 months after post-partum conception. Two non-lactating females culled with their 4,5 month and 7 month old infants support this conclusion.

5.3.4.5 Foetal sex ratio

A total of 42 females were visibly pregnant, but only 36 embryos and foetuses could be sexed. Of these, 20 were males and 16 were females (125 males:100 females). This ratio does not significantly differ from parity. No incidence of twinning was recorded.

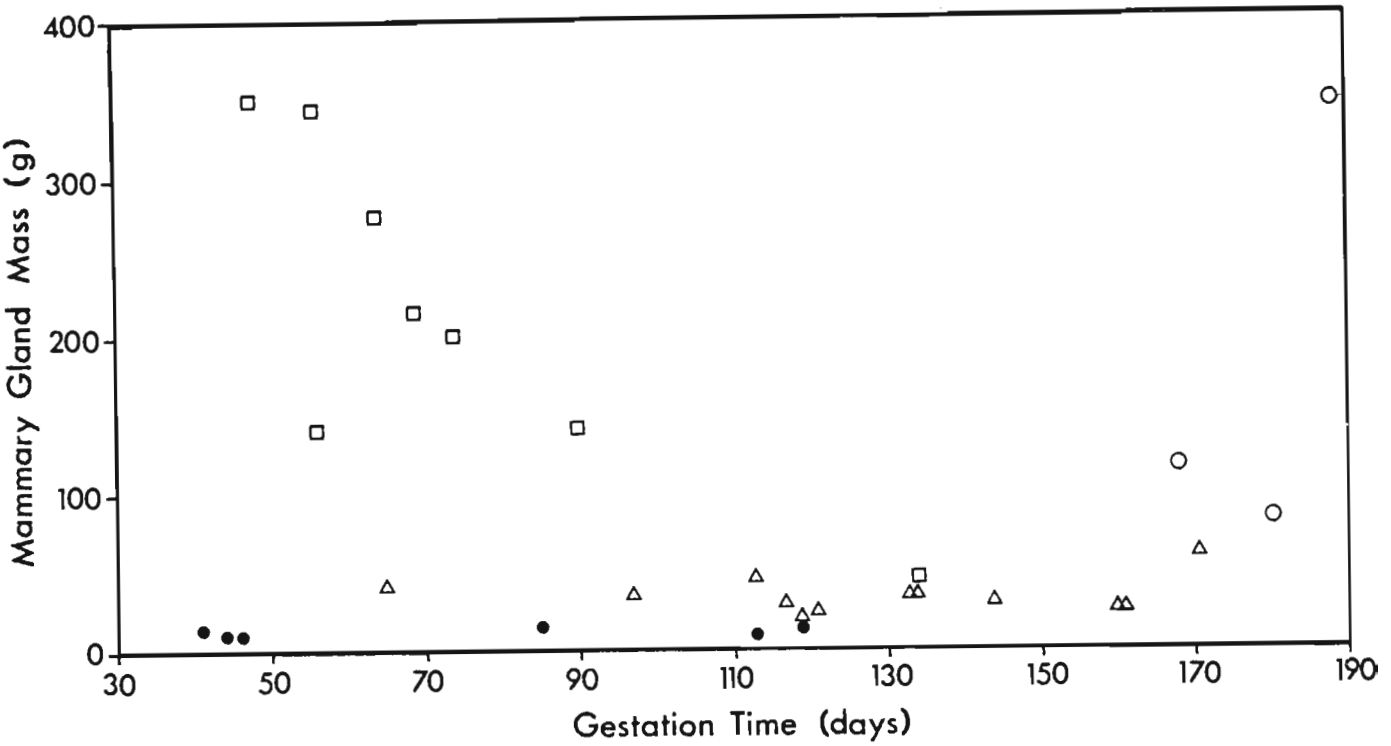


FIGURE 5.27 Variation in mammary gland mass with duration of pregnancy in female duiker (open square - lactating and parous; open triangle - non-lactating, parous; open circle - gland secreting colostrum; closed circle - non-lactating, nulliparous).

5.3.4.6 Seasonality of conceptions and births

As in bushbuck, foetal ages were determined using the Huggett and Widdas (1951) equation where gestation was taken as 191 days and an average mass at birth as 1 650g. This latter value was the mean derived from the mass of two full term foetuses of 1 648g and 1 666g and a neonate of 1 900g, all from Weza, together with the birth mass detailed in Wilson (1968) and Wilson et al. (1984).

The parturition dated calculated from all embryos and foetuses collected between September 1980 and October 1984 are illustrated in Fig. 5.28, together with the monthly distributions of culled, mature females. Distinct birth peaks were apparent during this period, but these did not exhibit any degree of regularity and simply followed the disproportionate distribution of culled females. Combining

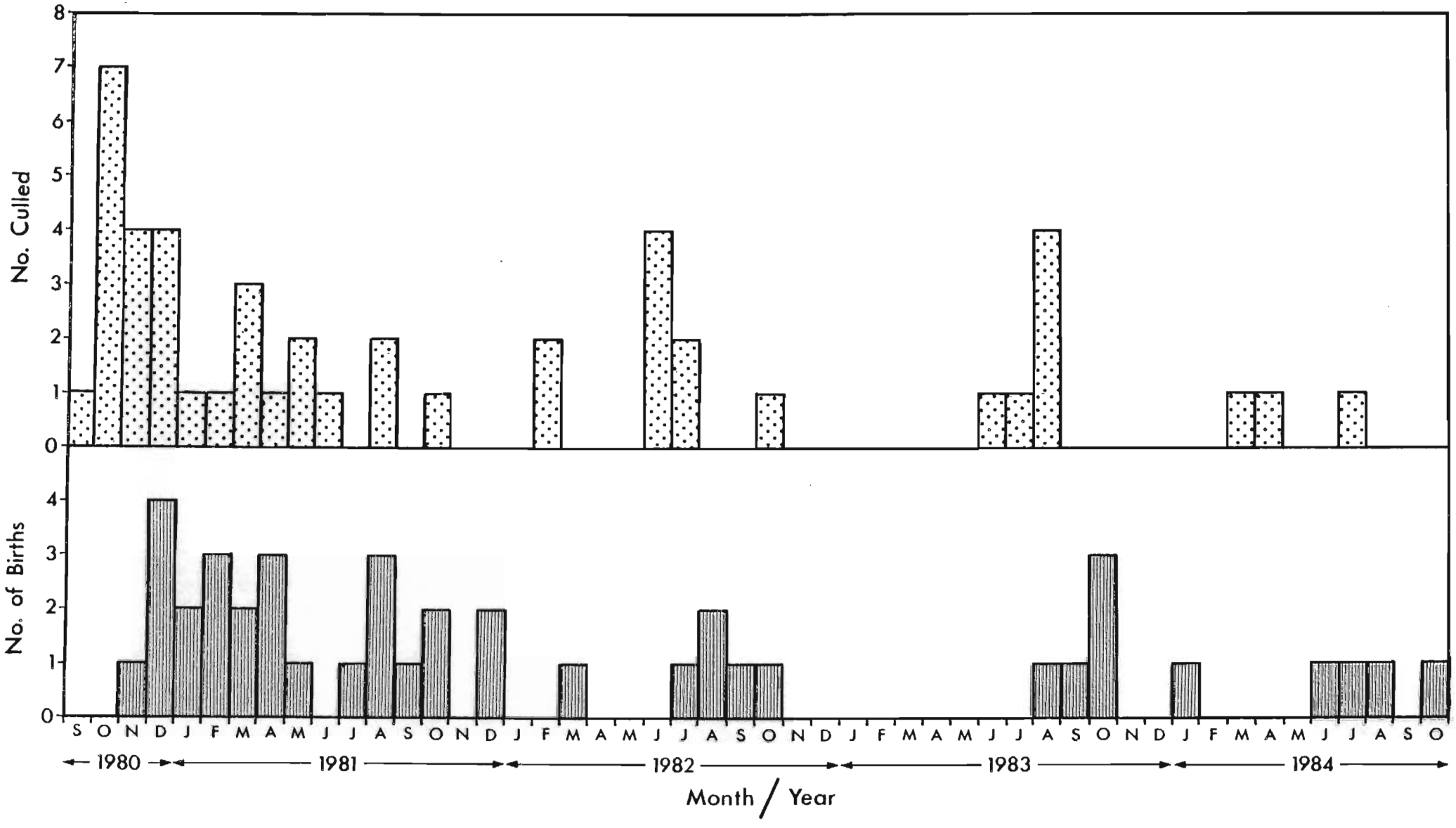


FIGURE 5.28 The frequency of (a) culled mature females and (b) parturition dates (determined from foetal age) of duiker from the period September 1980 to October 1984.

these data over one calendar year revealed that 27 of the 41 births (66%) would have occurred between July and December (Fig. 5.29) when 61% of all females over the age of 10 months were collected (Fig. 5.29). Because of the unequal numbers of females shot each month (Fig. 5.30), pregnancy rates could not be compared meaningfully at monthly intervals, and consequently data were combined on a seasonal basis (Fig. 5.31). Using Bailey's (1959) "d" test there were no significant differences between the pregnancy rates of females examined in consecutive seasons, or between females examined in January to June compared to those of July to December.

Although the proportion of females lactating increased during spring and summer (Fig. 5.31) these were not statistically analysed as other external factors, such as seasonal fluctuations in infant and juvenile mortality rates, may have influenced the incidence of lactation.

Birth dates were also determined by subtracting the ages of all duiker younger than one year from the month in which they were collected. Although births determined in this manner occurred throughout the year with the exception of September and November, 71% of these occurred in the first half of the year (Fig. 5.32). These results therefore differ from the birth data obtained from foetal ages (Fig. 5.29) which by subtraction of the gestation period, reveal that the period from January to June is the time when most females (68%) conceived (Fig. 5.33).

5.3.4.7 Field observations

Insufficient and/or irregular resightings and recaptures of marked postpubertal female duiker precluded assessments of ages at first parturition and lambing intervals from field observations. Captured females were nursing infants in six of the seven months that they were examined, the only exception being in May when a female carrying a full term foetus was immobilized. Two other captured duiker has full term foetuses in November, and one of these females gave

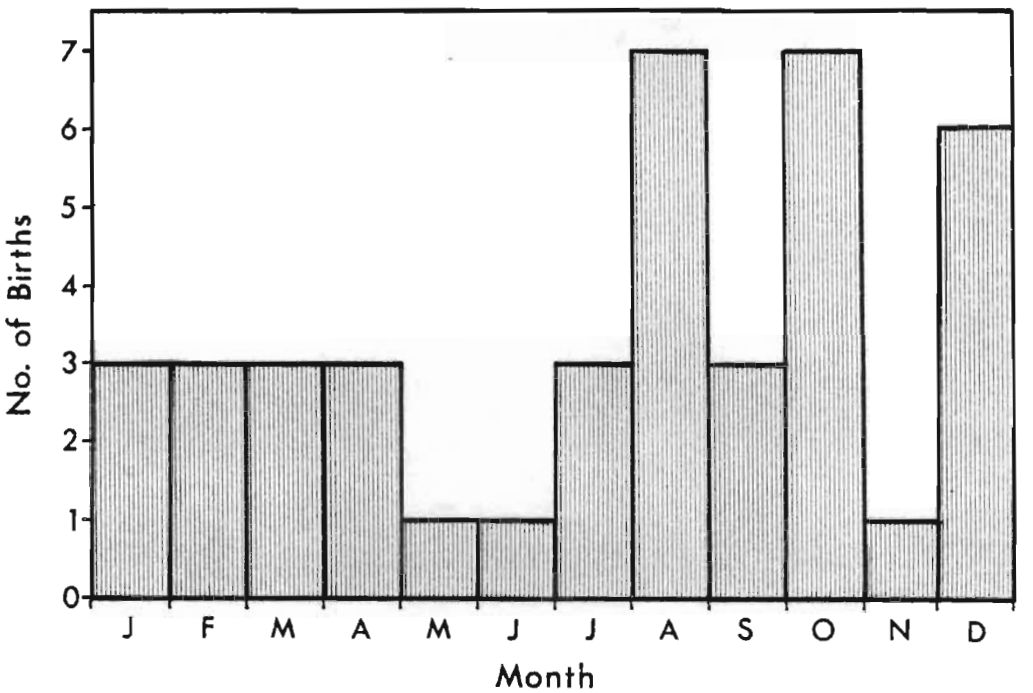


FIGURE 5.29 Accumulated parturition dates of duiker determined from foetal age.

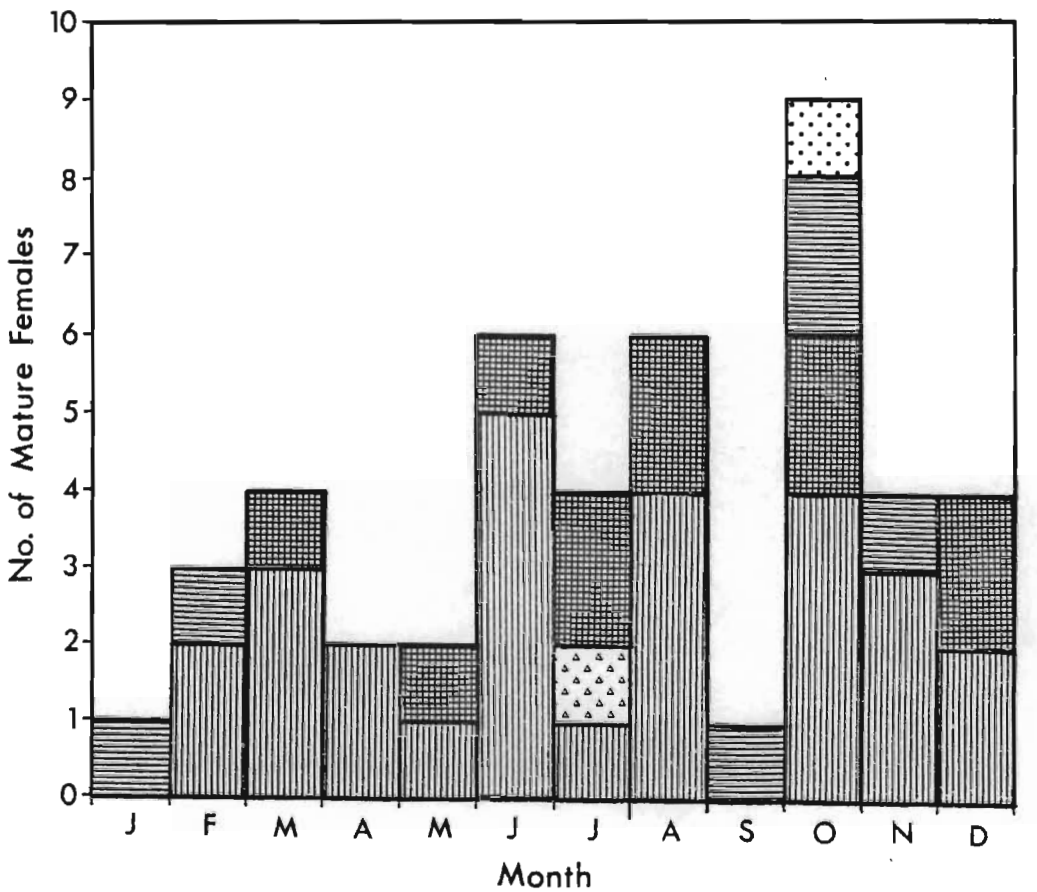


FIGURE 5.30 Variation in the number and reproductive status of mature female duiker examined each month. (= pregnant; = pregnant and lactating; = lactating; = not pregnant, not lactating; = status unknown).

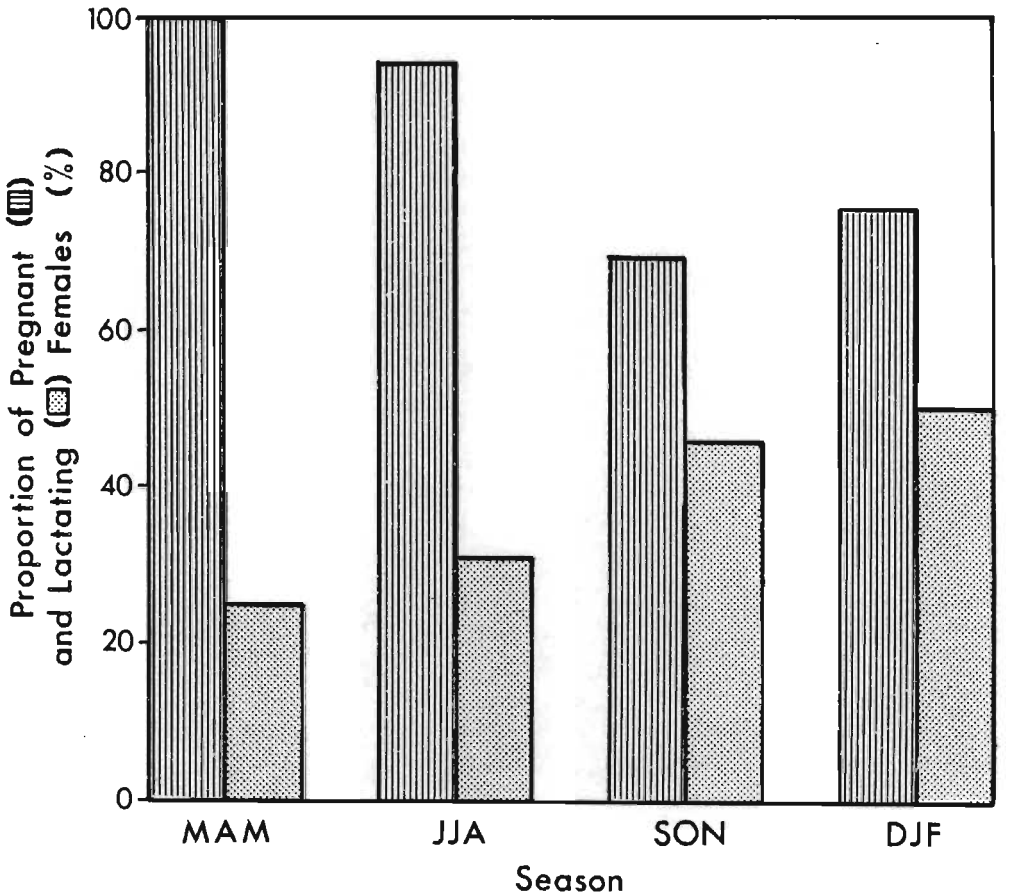


FIGURE 5.31 Seasonal changes in the proportions of pregnant and lactating female duiker.

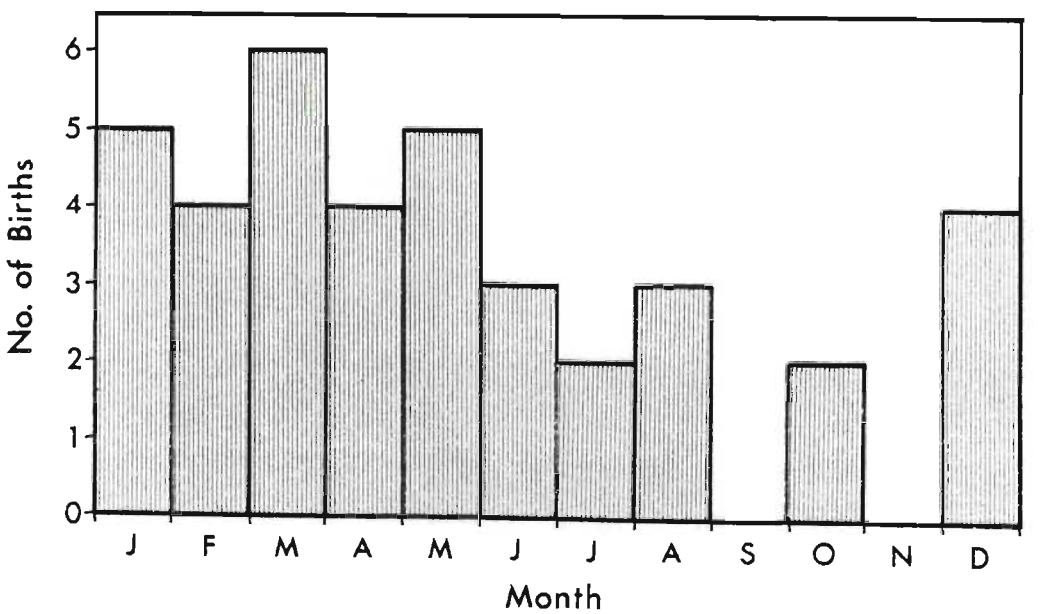


FIGURE 5.32 Birth dates of duiker determined by back-dating the estimated ages of infants and juveniles.

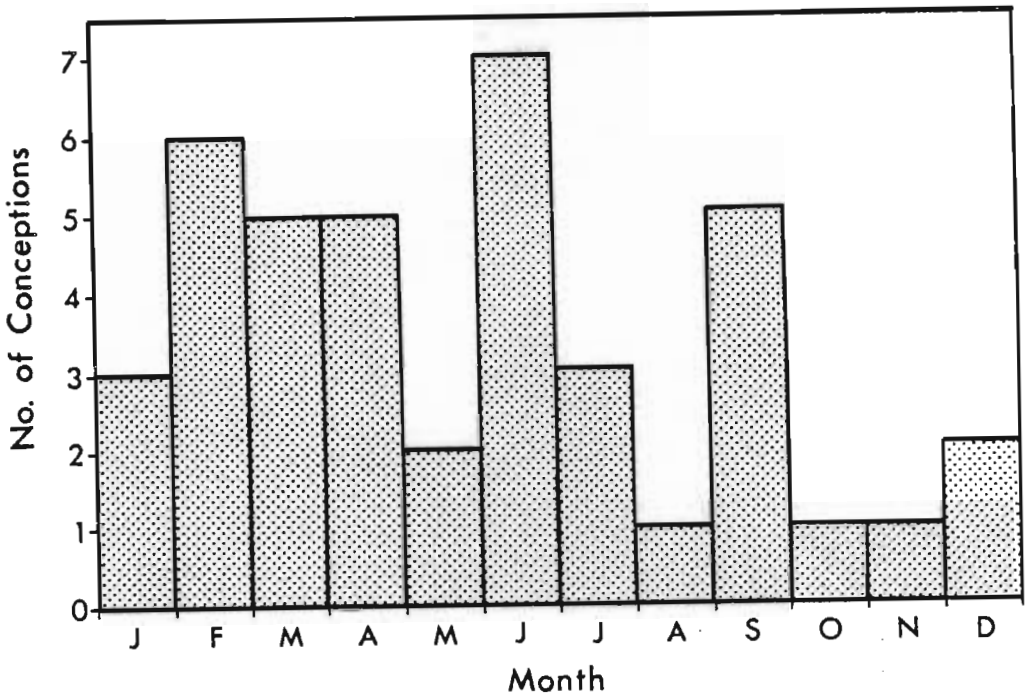


FIGURE 5.33 Accumulated conception dates of duiker determined from foetal age.

birth three days later (mother and infant detected by radio telemetry). Another infant, with remains of its umbilical cord still attached and therefore probably less than 10 days old (Sikes 1958) was found in July.

The proportions of infants, expressed as a percentage of all duiker seen each month, showed considerable variation during the first year of field work. No infants were observed during March and April (when visibility was most restricted by dense vegetation) or in November, while the highest proportion was recorded in December. For the remaining months, infants represented 1 to 4% of the total duiker sightings (Fig. 5.34).

5.4 DISCUSSION

5.4.1 Puberty and Sexual Maturity

Results from this study have shown that there is a clear distinction between the body mass, combined testes mass and mean seminiferous tubule diameters of pre- and postpubertal males of both species at Weza, and that once spermatogenesis

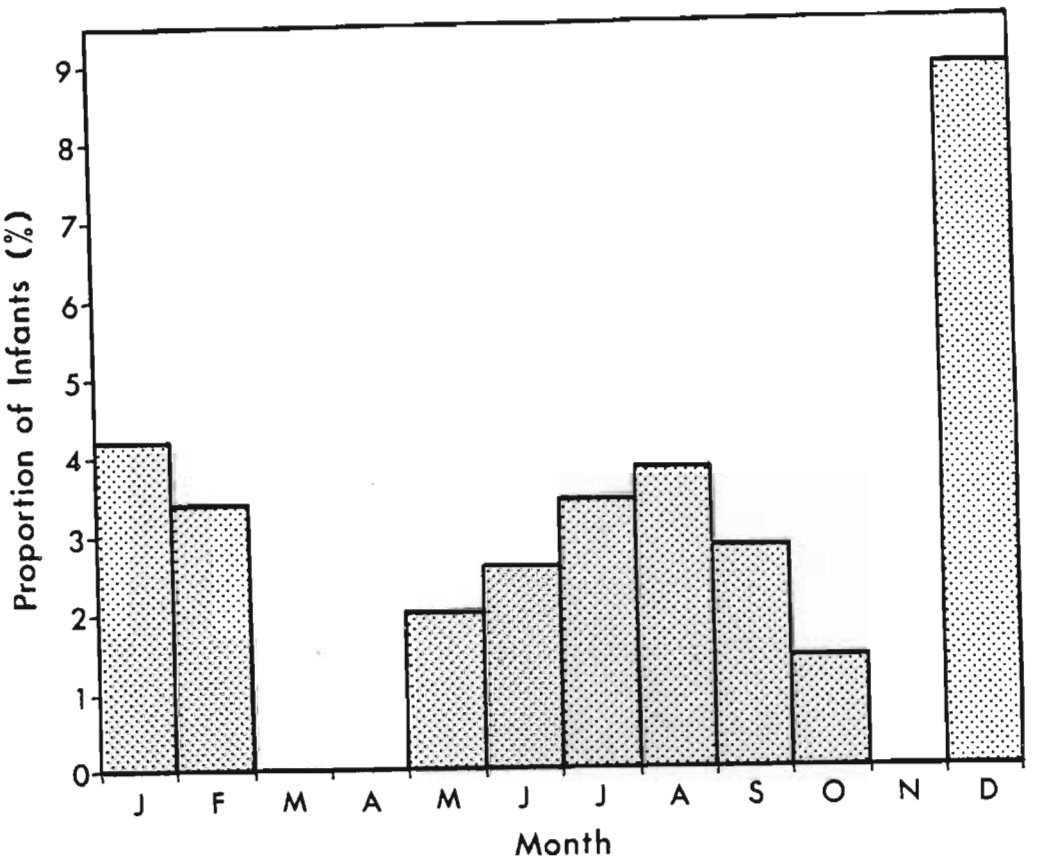


FIGURE 5.34 Sighting frequencies of infant duiker between November 1980 and October 1981 expressed as a proportion (%) of all duiker seen per month. (Total number of observations = 708).

is initiated, rapid growth in the male reproductive organs ensues. The mean age at which bushbuck attain puberty (11 months) and the dimensions of the reproductive organs at this age, show close agreement to those values obtained from bushbuck inhabiting other areas (Allsopp 1970; Morris 1973; Simpson 1974c). Bushbuck males at Weza attained puberty just prior to the visible development of secondary sexual characteristics including horn growth and a darkening of the pelage (Chapter Three). In contrast, puberty in the less sexually dimorphic duiker was attained at an average of 9,5 months, when horns had grown to an average of 67% of their asymptotic value, suggesting that in this species androgenesis preceded spermatogenesis by approximately five months (Chapter Three). Male duiker attained puberty at an earlier age than male bushbuck, but spermatogenesis commenced when male duiker had attained approximately 80% of their asymptotic body mass, while in bushbuck, spermatogenesis was

initiated at a much earlier stage of development, when males were on average 30% of their potential mass (Chapter Three). Possible reasons for these differences may, in part, be due to the contrasting strategies of mate acquisition exhibited by these two species (Chapter Eight).

That all of the mature females examined were heavier than their immature contemporaries, suggests that the age of puberty in these two species is strongly influenced by body mass, and thus ultimately by growth and condition. The relationship between puberty and body mass was not so obvious when females of different ages were considered, but since the size and condition of pregnant females could only be determined at their time of collection, and not when they had conceived, these are not directly comparable with immature females. Nevertheless, taking the mean age of attainment of puberty as nine months in the duiker and 19 months in the bushbuck, females of both species matured at a similar stage of development, when they were both approximately 75% of their respective asymptotic mass (Chapter Three).

Female bushbuck from Weza attained sexual maturity at a considerably later age than the wild population studied by Morris (1973) and the captive bushbuck of von Ketelhodt (1976), but at a similar age to females from several other populations (Wilson and Child 1964; Allsopp 1970; Dittrich 1977; Mentis 1972). Previous studies of duiker have been less precise in their approach to estimations of the age of attainment of puberty and sexual maturity, and have further been hampered by inaccurate methods of age determination and highly variable periods of gestation. Nevertheless, the results of this study which suggest a very rapid attainment of sexual maturity in both sexes, are in general accord with those of previous studies (Dasmann and Mossman 1962a; Wilson and Clarke 1962; Child and Wilson 1964; Wilson and Roth 1967; Mentis 1972).

Assuming that nutrition is the proximate factor responsible for variations in the age of sexual maturity (see Sadleir 1969a, 1969b; Verme 1969; Lincoln *et al.* 1970;

Mitchell 1973; Mitchell and Brown 1974; Wegge 1975; Staines 1978; Albon et al. (1983), comparisons between these two species from Weza and from other areas suggest that food resources may be limiting the onset of breeding to a greater extent in bushbuck than in duiker. This concept is considered further in Chapter Ten.

5.4.2 Ovulation and Implantation

In both species, the mass of the heaviest ovary was highly indicative of reproduction status, with heaviest ovaries from pregnant and lactating females, intermediate values from pregnant or lactating females, and the lightest ovaries from reproductively active or prepubertal individuals. Assuming that an increase in ovarian mass was directly attributable to luteal tissue production, corpora lutea from both bushbuck and duiker remained relatively constant in size throughout pregnancy. Morris (1973) came to a similar conclusion in his bushbuck study, and the same trend has been noted in a number of other species, including elephant (Hanks and Short 1972) and waterbuck (Spinage 1969b), but not in wildebeest where luteal tissue increases towards the end of pregnancy (Attwell and Hanks 1980) or in impala where corpora lutea increase in volume and then regress during pregnancy (Kayanja 1969).

In bushbuck, ovulation and implantation appeared to be fairly evenly distributed between the left and right ovaries and horns of the uterus respectively, but ipsilateral implantation was much more common (86%) than contralateral implantation. Simpson (1974c) reached a similar conclusion, except that all of the female bushbuck he examined exhibited ipsilateral implantation, while a tendency towards ipsilateral implantation is common in several other small antelope species (Kerr and Wilson 1967; Hofmeyr and Skinner 1969; Wilson and Kerr 1969).

In contrast, although ovulation was almost equally distributed between left and right ovaries, implantation in

the duiker always occurred in the right horn. This phenomenon has also been noted by Child and Mossman (1965) Symington and Paterson (1970) and Smithers (1971) and although the physiological mechanisms and adaptive significance are poorly understood, unilateral implantation commonly or invariably occurs in a number of other ungulate species (Buechner 1961; Robinette and Child 1964; Hofmeyr and Skinner 1969; Kayanja 1969; Chapman and Dansie 1970; Hvidberg-Hansen 1970).

5.4.3 Fertility, Performance and Parturition Intervals

Despite abnormalities in the testicular growth of five male duiker, all of the postpubertal animals examined during this study were fertile, and senescence has yet to be reported in either of these two species (Allsopp 1970; Morris 1973; Simpson 1974c).

Both bushbuck and duiker had remarkably high rates of reproduction during the study period, with only one postpubertal female duiker not actively breeding. Comparisons between the reproductive performances of bushbuck and duiker at Weza with those from other populations were hampered by differing methods of evaluation. Nevertheless, where such comparisons were valid, these demonstrated that the specific breeding rates (i.e. the proportions of mature females that were either pregnant and/or lactating) attained by bushbuck at Weza (100%) were appreciably higher than those from other areas, which ranged from 72% to 91% (Wilson and Child 1964; Allsopp 1970; Simpson 1974c). Specific conception rates showed a similar trend, where 77% of all postpubertal females at Weza were pregnant (Table 5.8), compared to 46%-68% of the mature females examined by Wilson and Child (1964), Allsopp (1970), Morris (1973)and Simpson (1974c). The specific breeding rate of duiker at Weza was almost as high (98%) as bushbuck and although Smithers (1971) recorded a similar value from a population in Botswana, considerably lower values of 53% and 66% were obtained from a population reported to have a high reproductive rate (that

was induced by intensive hunting) by Wilson and Clarke (1962) and 47% determined from Wilson and Roth's (1967) data for each year of their study (when again, the effects of hunting were reported to have resulted in an increased rate of breeding).

Although female bushbuck at Weza attained sexual maturity at a later age than those from several other areas, and may therefore have survived on a lower plane of nutrition, the high reproductive rates recorded in this study infer that once mature, the reproductive cycles of both bushbuck and duiker at Weza are not influenced by diet or condition, even though both of these fluctuate considerably during the year (Chapter Four and Chapter Six).

Relatively short intervals between pregnancies (39 days estimated for bushbuck and 35 days for duiker) corroborate this conclusion, since addition of their respective gestation periods reveals that bushbuck and duiker both produce on average 1,6 young per annum. Similar lambing intervals have been quoted in several previous studies, yet fecundity rates in these studies have been considerably lower than at Weza; these anomalies warrant further consideration. Simpson (1974c) maintained that parturition intervals of 180 days were realised in his bushbuck population and that these accounted for two apparent and equally spaced breeding peaks during the year. While there is no doubt that bushbuck, and indeed a number of other ungulate species (Dittrich 1974, 1978) are capable of immediate postpartum conception, all available evidence from both wild and captive animals suggest that this is an unusual event and that intervals of one to three months between parturition and conception are more common (Table 5.3). Further, Simpson's conclusions regarding a parturition interval of 180 days is highly speculative and based on the single observation of one adult female that was "lactating fully" and was visibly considered to be in oestrus. If his raw data regarding the proportions of pregnant and non-pregnant mature females are substituted into the formula of Short (1966), mean parturition intervals of 263 to 315 days are evident from the three populations he

examined, with an overall value of 307 days. This is significantly longer than his estimated period of 180 days.

Morris (1973) calculated one minimum parturition interval of 225 days from the ages of a foetus and an infant from the same female, and quoted several other intervals determined from observations of captive animals elsewhere. Again, analysis of his raw data regarding pregnancy rates suggests a mean parturition interval of 391 days. Allsopp (1970) suggested a mean parturition interval of 285-315 days in his population that had a specific breeding rate of 91%. His method of determining parturition intervals was somewhat subjective however (see 5.1.1.2.6) and re-examination of his data yields a shorter mean interval of 263 days. Wilson and Child (1964) did not calculate lambing intervals in their study but identical treatment of their data indicates a period of 300 days.

Parturition intervals have not been published for other wild populations of duiker, but analyses performed during this study indicate mean intervals of 233 days (data from Smithers 1971), 338 days (data from Wilson and Clarke 1962) and 410 days (data from Wilson and Roth 1967). With the exception of the population from Botswana (Smithers 1971) these are appreciably longer than the mean interval of 226 days recorded from Weza.

Thus, while the parturition intervals determined from this study are in close agreement with intervals of captive animals (Mentis 1972; Morris 1973; Dittrich 1974; von Ketelhodt 1976, 1977; Kingdon 1982) they are considerably shorter than those determined from other wild populations when the method of evaluation is standardised, and reinforce the conclusion that both bushbuck and duiker attain their full reproductive potential at Weza. This conclusion is considered further in Chapter Ten.

5.4.4 Field Observations

The collection of reproductive data in the field was

undertaken in conjunction with other specific objectives of the total study, including censuses, capture operations for marking and radio telemetry purposes, and during the collection of habitat preference data. Consequently, these were collected by less exacting means than during post mortem sampling, and were therefore probably less precise. The collection of these data was also restricted by unequal sampling throughout the year, and seasonal fluctuations in both capture success rates and in ranges of visibility. Other variables that could not be quantified but that may have biased conclusions based on observations in the field included the lying-out, or concealment period of offspring (which may continue for several months, Kingdon 1982) and neonatal and infant mortality rates.

In spite of all of these limitations, parturition intervals of bushbuck determined from field data average 243 days and were thus only slightly longer than those determined from the culled sample. The duration of lactation estimated by field observations also supported the estimates of five to seven months obtained from culled females. Ages at first parturition estimated from field data were considerably older than those from culled individuals however, and although some of the former may have been overestimated (by lying-out behaviour of their young etc.), fairly comprehensive records suggested that in several instances, females did not give birth to their first young until at least 30 months of age, and therefore only conceived when at least two years old. Reasons for these differences in the attainment of sexual maturity are not known. Several other studies have shown how sexual maturity and/or fecundity may be delayed by inadequate nutrition (as discussed earlier) that may result from inferior or marginal habitats (Lowe 1969; Wegge 1975; Staines 1978) or from increasing intraspecific competition (Klein 1970). It is therefore interesting to note that all of these females that bred for the first time when at least two years old lived entirely in prime habitats (as determined by habitat preferences, see Chapter Seven) that had higher densities of bushbuck than any of the other habitats surveyed (Chapter Nine). The mean parturition interval of 243 days

was also determined from mature females co-inhabiting the same area. Thus, if the onset of sexual maturation was prolonged by the influences of environmental factors, these same factors probably had little effect on subsequent reproductive rates, which must be regarded as minimal values since infant mortality rates could not be assessed.

5.4.5 Seasonality of Conceptions and Births

Numerous studies have demonstrated that changes in testes mass, epididymides mass and seminiferous tubule diameters are reliable indicators of reproductive seasonality in male ungulates. These changes are probably most pronounced in several cervid species where active spermatogenesis lasts only for four months (Bubenik et al. 1977) and although spermatozoa may remain viable for over six months, males are in a state of reproductive quiescence for approximately three months of the year. In such species, the adult stag undergoes reproductive changes each year that resemble pubescence (Lincoln 1971).

Less pronounced, but equally significant changes have been noted in the male reproductive organs of many other species exhibiting seasonal breeding, and are characterised by maximum mass and dimensions just prior to or during the peak conception period, followed by a rapid decline in size after the rut (Skinner 1971a, 1971b; Skinner et al. 1974; Hanks et al. 1973; Smuts 1976b; Mirarchi et al. 1977b). These changes are also evident in those species that are capable of breeding throughout the year but nevertheless exhibit seasonal peaks in reproduction (Skinner et al. 1971; Skinner et al. 1974; Skinner 1978), but are less obvious or absent in those species that breed irregularly or continually throughout the year (Spinage 1969b; Hall-Martin et al. 1975).

Since the reproductive organs of fully mature bushbuck males showed no significant seasonal variations in mass or size, it must be concluded that males of this species exhibited no seasonality in their physiological ability to

reproduce. A similar conclusion can be drawn from the reproductive organs of male duiker, for although testes and epididymides mass were greater in summer than in spring, the same trend was not evident in seminiferous tubule diameter, and none of these criteria of sexual activity deviated significantly from the overall values obtained from all fully mature males.

Although initial inspections of parturition dates of both bushbuck and duiker suggested a seasonal peak in breeding, these were clearly biased by unequal monthly samples as summarised for bushbuck in Fig. 5.35. Spinage (1969b) has also demonstrated how analyses of seasonality may be seriously biased by varying intensities of sampling. In order to obviate these limitations, seasonal pregnancy rates were compared (Figs. 5.20 and 5.31) and showed no significant differences, suggesting that females of both species are reproductively active throughout the year. Mean parturition intervals of 222 and 226 days for bushbuck and duiker respectively also infer that the timing of breeding is not

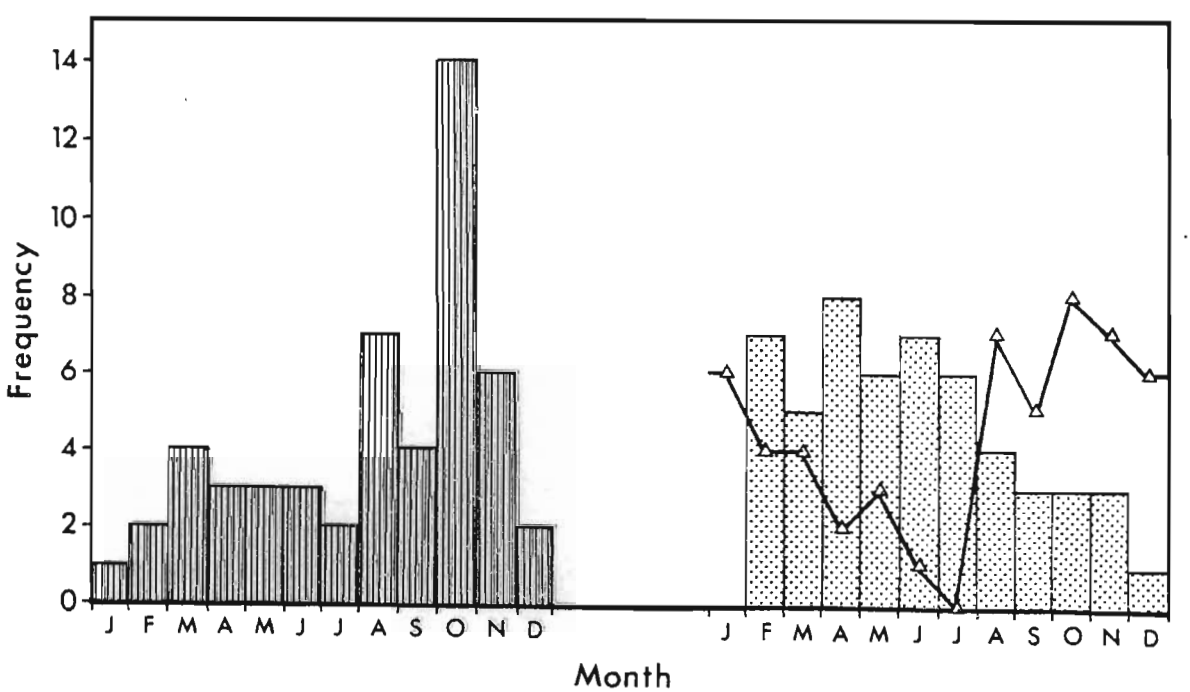


FIGURE 5.35 The monthly distribution of pregnant females (▥), conceptions (▩) and births (△—△) of bushbuck culled at Weza, 1980-1984.

influenced by periodic environmental cues. Less direct, but nevertheless supportive evidence of aseasonal breeding was obtained by back-dating the ages of culled juveniles (Riney and Child 1964; Robinette and Archer 1971) and from the proportions of infants seen each month, even though these latter estimates reflect survival rather than birth rates, and may further be biased by lying-out behaviour and variable ranges of visibility during the year (Wilson and Clarke 1962; Robinette and Archer 1971; Anderson 1978). Therefore, in conclusion, there is little evidence to suggest that either species exhibits seasonality, and both bushbuck and duiker should rather be considered as continuous breeders at Weza.

In contrast, seasonal breeding has been described in all previous detailed studies of bushbuck. Since bushbuck at the southern limit of their range (e.g. at Weza) are likely to experience much greater fluctuations in climatic conditions and environmental resources during the year than populations nearer to the equator, these finding initially appear to be contradictory and require further discussion. Allsopp (1971) determined conception and parturition dates from foetal ages of 24 pregnant females and concluded that distinct peaks in the numbers of births occurred in February and September. Apart from basing his conclusions on a rather small sample size, this was not evenly distributed throughout the year (Fig. 5.36). Wilson and Child (1964) concluded that bushbuck in Zambia gave birth throughout the year, but Allsopp (1971) re-examined their data (15 foetuses) and concluded that "distinct peaks occur for birth in December and to a lesser extent in April". The distribution of these births is illustrated in Fig. 5.36, where the "distinct peaks" represent an increase of two births over other months of the year. Since foetal ages calculated from the Huggett and Widdas (1951) equation must be treated as approximations only (Guy 1983), Allsopp's (1971) conclusions are not considered to be valid. Allsopp (1971) further suggested that the foetal growth velocity "a" may "determine breeding seasonality by varying to accommodate environmental conditions when birth at a particular time of year is most advantageous". This argument is also considered to be

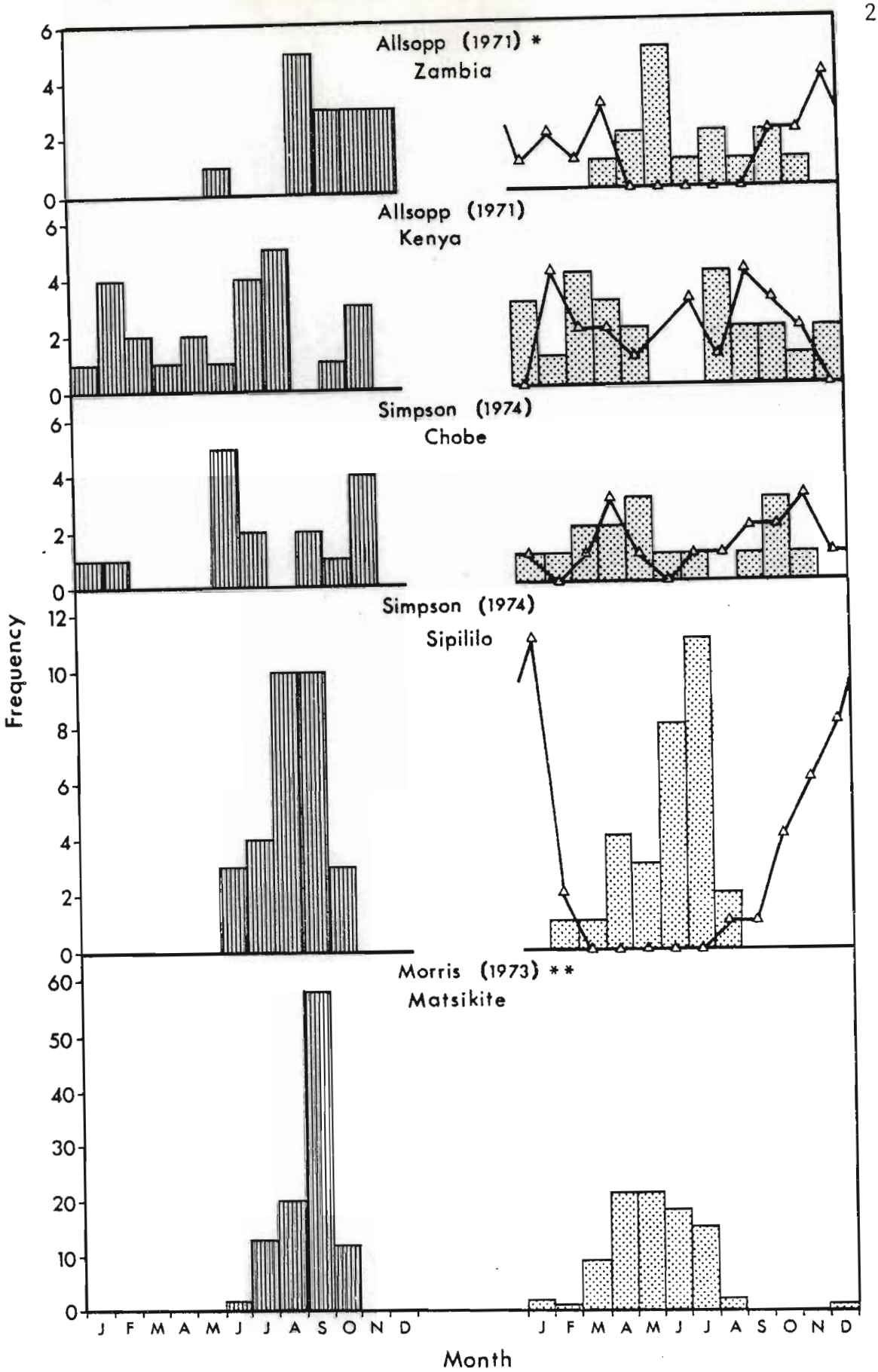


FIGURE 5.36 Previous breeding studies of bushbuck showing monthly variations in the numbers of pregnant females examined ( ), and frequencies of conceptions ( ) and births (△ △). (* Allsopp 1971 - original data from Wilson and Child 1964; ** Morris 1973 - birth dates not determined).

spurious since the value of "a" is simply a function of foetal mass at a known interval of gestational age.

Simpson (1974c) also calculated conception dates from foetal age and concluded that peak rutting occurred during May and October at Chobe, and since parturition intervals of 180 days were apparently evident from this population, birth peaks also occurred during these months. Again, his sampling was uneven throughout the year and was based on 16 foetuses (Fig. 5.36). In his study of another population at Sipililo, Simpson (1974c) found a peak in conceptions during April and May but his sample was confined to just five months of the year (Fig. 5.36), and inexplicably included more pregnant females than he showed conception dates for.

Morris (1973) and Morris and Hanks (1974) found a peak of conceptions in April and May, but again their sampling was confined to five months of the year (Fig. 5.36). Morris (1973) also examined monthly pregnancy rates, and since these varied considerably each month he suggested that "a certain degree of seasonality of breeding occurs". Re-examination of his data indicated that monthly variations were not as pronounced as he had illustrated, and ranged from 28% in June to 61% in September, but again these rates were based on different monthly totals of culled females. Morris (1973) was also unable to detect similar rates of pregnancy in monthly samples from an adjacent population (which according to Simpson (1974c) showed seasonality) and suggested that a shift in the peak of breeding had occurred in this latter population. Such shifts would of course be inevitable if the seasonal breeding patterns and parturition intervals quoted by all these authors are realised.

It is therefore contested that the conclusions from all of these studies have been biased by either inadequate or unequal sample sizes and that reproductive seasonality has yet to be unequivocally demonstrated in either bushbuck or duiker. The distribution of births of these two species is considered further in Chapter Ten.

CHAPTER SIX
FEEDING ECOLOGY

6.1 INTRODUCTION

Understanding dispersion, i.e. the way in which an animal occupies its range and the processes bringing this about (Wynne-Edwards 1962), is important for wildlife management for a number of reasons. Firstly, the animal's growth, life-expectation and fertility are affected by where it chooses, or is obliged to live, and as shown in the three preceding chapters, more specifically by the food resources that are available to it. Secondly, its dispersion brings it into contact with human interests; certain species of wildlife may be welcome as an asset or resource in some areas, but unwelcome as a potential or real cause of damage in others. Finally, the area an animal occupies does not necessarily reflect is optimum preferences or requirements, but is more often the result of the interactions between the animal's behaviour and limiting environmental factors. The major factors influencing local distributions of ungulates include the suitability of the habitat in providing adequate food, nutrition and cover, the degree of disturbance from both man and as a result of interactions with other herbivores, and the level of social and spatial organisation exhibited by each ungulate species (Mitchell et al. 1977). This chapter considers the feeding ecology of bushbuck and duiker in a forest environment, with an emphasis on the impact these antelope have on silviculture. Although inter-related, the habitat requirements and preferences of these two species are, for convenience, examined in the following chapter together with the effects of forestry management practices, while Chapter Eight considers levels of social and spatial organisation.

6.1.1 A Review of Methods Currently Employed in the Determination of Herbivore Diets

There is a wide variety of established methods that are

available to the biologist wishing to determine the diets of wild herbivores. However, all of these have limitations (Fitzgerald and Waddington 1979; Smith and Shandruk 1979; Holechek et al. 1982a). The wildlife biologist should therefore be aware of these constraints before embarking on such a task, and decide which method is best suited to his objectives and to the animals under study. The relative abundance of his study animals, their relative tameness and cycles of activity, the presence of other sympatric herbivores, and the vegetational structure of their habitats may all influence the quality of his results. Numerous authors have listed the merits and disadvantages associated with the methods used to determine herbivore diets, and these are briefly reviewed below. However it should be noted that the reasons one biologist gives for rejecting any single method might be ignored in another study where alternative techniques are even more restricting. Consequently, opinions regarding the utility of each method are often at variance.

6.1.1.1 Utilization techniques

Utilization is one of the oldest approaches used to evaluate the diet of herbivores. The advantages of this approach include speed and the fact that it provides information on where and to what extent a habitat is being utilized (Holechek et al. 1982a). Various utilization techniques have been reviewed by Smith et al. (1962) cited in Holechek et al. (1982a) and Martin (1970). These include the evaluation of differences before and after foraging or between grazed and ungrazed plots or plants; the measurement, correlation and regression of factors related to utilization; and methods based on general observations and comparisons with predetermined standards of use (Martin 1970).

Ocular estimates of utilization (e.g. Crouch 1968; Anderson et al. 1972c; Hjeljord 1973; Blair and Brunett 1980) are subject to observer error and personal biases (Smith and

Shandruk 1979). More quantitative data may be obtained by the feeding site method (e.g. Allen 1968; Bayless 1969; Martinka 1969; Kohn and Mooty 1971; Constan 1972; Smith and Malechek 1974; Peek et al. 1976; Wydeven and Dahlgren 1983) which is essentially similar to the bite-count approach (see below) except that observations are made of the vegetation rather than of the foraging animal. Unless sampling design is carefully considered, this method may provide meaningless information (Wallmo et al. 1973). Several authors have confined this approach to the examination of woody browse, i.e. the twig-count method (e.g. Shafer 1963; Stickney 1966; Lay 1967; Segelquist and Green 1968; Knierim et al. 1971; Van Ballenberghe and Peek 1971; Tilton and Willard 1981). However the method becomes insensitive under heavy utilization levels (Jensen and Scotter 1977) or where rebrowsing occurs (i.e. browsing on an already browsed twig (Nystrom 1980)), and in such instances twig measurement data provide a superior and more quantitative means of assessment, albeit with increased effort and associated costs (Hjeljord 1973; Jensen and Scotter 1977). Twig measurements are usually confined to diameters recorded at the point of browsing and can be converted to mass of forage eaten using (species-specific) diameter-mass regression equations (Telfer 1969, 1972; Peek et al. 1971, 1976; King 1975; Wetzel et al. 1975; Ferguson and Marsden 1977; Telfer and Cairns 178).

Several factors may seriously influence results obtained from these utilization techniques. Plant species may differ in their seasonal rates of growth and in their response to grazing (Martin 1970) while exclosures used to estimate herbage utilization are not always reliable since grazed plants may perform differently to ungrazed ones (Mitchell et al. 1977). This latter problem is further confounded by the fact that exclosures in the form of cages may modify the microclimate (Martin 1970; Holechek et al. 1982a). Utilization is difficult to detect when use is light, and when more than one herbivore is present it may not be possible to separate their effects (Borowski and Kossak 1975; Mitchell et al. 1977; Smith and Shandruk 1979; McInnis et al. 1983).

Inaccurate estimates of consumption may also result from "invisible utilization" such as occurs when the whole plant is pulled up or consumed by the foraging animal (Healy 1971; Smith and Shandruk 1979), or in rapidly growing plants where regrowth obscures evidence of previous grazing or browsing (Martin 1970), although regrowth may not be selected to the same extent as primary growth (Miquelle 1983). A further category of invisible utilization is the seasonal consumption of deciduous plants or plant parts, including leaves of deciduous shrubs and trees, and many types of fruits. Once the deciduous plant part has fallen, the amount taken by herbivores cannot be estimated by conventional means. An opposing source of error which may overestimate actual forage consumption is that of distinguishing between foods consumed by study animals and losses to other influences. Trampling and weathering, climatic influences, normal losses of deciduous plant parts and use by other herbivore species are examples of such "extraneous utilization" (Martin 1970). Finally, utilization estimates do not provide precise information on when or how often a forage species is used, nor do they show close agreement with data obtained from fistulated animals (Holechek et al. 1982a). Any utilization technique has severe limitations when forage is actively growing and/or use is by more than one species of herbivore, and under these conditions, Holechek et al. (1982a) recommend the use of alternative means to determine the botanical composition of herbivore diets.

6.1.1.2 Direct observations of the animal

A widely practiced procedure in studies of the botanical composition of herbivore diets is direct observations of the foraging animal. The major advantages of direct observation include simplicity, ease of use and minor equipment requirements (Holechek et al. 1982a). Although the diets of wild animals may be assessed in this manner (e.g. White 1961; Hlavachick 1968; Jungius 1971a; Leuthold 1971a, 1978b; Constan 1972; Croze 1974; Conybeare 1975; Guy 1975, 1976;

Field and Ross 1976; Grimsdell and Field 1976; Rodgers 1976; Sauer et al. 1977; Krausman 1978; Owen-Smith 1979; Owen-Smith et al. 1983), it is often difficult to make detailed observations at night or in densely-structured habitats (Hofmeyr 1970; Mitchell et al. 1977). In addition, wild animals are often difficult to locate and approach closely enough for accurate observation, and difficulties in species identification and quantification of how much of a plant was consumed are important problems associated with this technique (Talbot 1962; Mitchell et al. 1977; Leuthold 1979; Holechek et al. 1982a). These problems may be reduced or eliminated with the use of enclosures (e.g. Dunkeson 1955; Miller 1968; Segelquist and Green 1968; Kie et al. 1980; Nystrom 1980; Owen-Smith et al. 1983) and/or tame animals (e.g. Field 1970, 1976; Wallmo and Neff 1970; Healy 1971; Nagy 1974; Nagy and Schwartz 1974; Stephens 1975; Urness et al. 1975; Schwartz and Nagy 1976; Schwartz et al. 1976, 1980; Kreulen 1977; Deschamp et al. 1979; Hobbs and Baker 1979; Kie et al. 1980; Stormer and Bauer 1980; Hobbs et al. 1981, 1983; Papageorgiou et al. 1981; Baker and Hobbs 1982; Crawford 1982; Collins and Urness 1983; Kossak 1983; Dailey et al. 1984; Thill 1984). However, Gill et al. (1983) found that the use of tame animals for feeding studies was expensive, laborious and time-consuming, while Bergerud and Nolan (1970) and Leuthold (1971b) have suggested that food selection by young animals may be influenced by imitation of older individuals and thus the food habits of hand-reared captive animals deprived of social contact with conspecifics may not accurately resemble the feeding strategies of their wild counterparts.

In addition, Bartmann et al. (1982) cautioned that prior foraging experience may significantly influence food choices of tame deer in unfamiliar habitats, and that selection may vary considerably between individual captive animals. Consequently, these authors recommended the use of as many tame animals as possible, ensuring adequate coverage of the area of interest, and maximum exposure of animals to study areas and forages. Further, Bartmann and Carpenter (1982) concluded that some period of preconditioning is essential

when tame deer are used in unfamiliar habitats, although "how long a period is required is not known and may be difficult to ascertain due to changes in individual preferences, plant phenology and plant availability over time". The influence of plant species diversity and availability on the diet selection of captive deer has been studied by Carpenter et al. (1979) but depends in part on the choice and size of the feeding site, stocking rates of tame subjects, and the level of utilization by other herbivore species (e.g. Krausman 1978; Kie et al. 1980; Monro 1982; Collins and Urness 1983; Hobbs et al. 1983; Dailey et al. 1984; Thill 1984).

In order to obtain quantitative information from direct observations of either wild or tame animals two different approaches may be employed. When the feeding minutes technique is used (e.g. White 1961; Bergerud and Nolan 1970; Field and Ross 1976; Owen-Smith et al. 1983), the time an animal spends feeding on each species is measured and is assumed to be proportional to the importance of the species in the diet (Bjugstad et al. 1970). In the bite-count approach, the number of bites taken from each species, rather than the duration of feeding time,is recorded (e.g. Wallmo et al. 1972; Stephens 1975; Guy 1976; Sauer et al. 1977; Leuthold 1978b, 1979; Dunham 1980; Baker and Hobbs 1982; Collins and Urness 1983; Dailey et al. 1984; Meyer et al. 1984). Animals ingesting more than one species at a time (Field 1970; Thill 1984) are likely to affect results in a similar manner irrespective of which method is used, while attempts to differentiate between mere nibbling and active feeding may further complicate diet selection assessments by observations (Bjugstad et al. 1970). Both quantitative methods have additional limitations. Wallmo et al. (1973) tested the accuracy of the feeding minutes technique and found that observers needed to be within 23 metres of foraging deer in order to identify accurately more than 80% of the ingested plants to species level. Owen-Smith (1979) noted that bite-size varied widely depending on whether kudu were feeding on woody plant leaves or ingesting whole forbs or creepers, and concluded that feeding time provided a closer measure of the quantity of food eaten than the number

of bites taken. Several authors have attempted to overcome the problem of varying bite-size by converting bites counted to dry mass, either by simple estimation in the field (Crawford 1982) or by the collection of simulated, hand-clipped "bites" that duplicate as closely as possible the amount and plant parts eaten by their tame subjects (Wallmo et al. 1972; Urness et al. 1975; Schwartz and Nagy 1976; Collins et al. 1978; Deschamp et al. 1979; Hobbs et al. 1983; Kossak 1983; Miquelle 1983; Dailey et al. 1984). Finally, the extent of training and experience of observers, the complexity of the plant communities under study, and the phenology of individual forage species are additional factors that may influence the accuracy and precision of the direct observation method (Holechek et al. 1982a).

As a result of all of these limitations, this method is better suited to the determination of which kinds of forage are selected or rejected, rather than determining the actual amounts of food plants that are consumed (Wallmo and Neff 1970).

6.1.1.3 Faecal analysis

Microhistological examination of faecal material is a technique widely used in the determination of animal diets and has become increasingly popular during the last decade (Korfhage et al. 1980; Holechek et al. 1982a; Gill et al. 1983; McInnis et al. 1983; Putman 1984). While much of the material in carnivore and omnivore faeces may be identified macroscopically (e.g. Johnson and Hansen 1977; Landers et al. 1979; Servheen 1983; Maehr and Brady 1984), the identification of herbivore dietary components is considerably more complex (Fitzgerald and Waddington 1979; Putman 1984). Herbivore faecal material is usually macerated and cleared in nitric acid to remove the opaque mesophyll before the diagnostic cellular structures of the epidermis can be detected under the microscope (e.g. Stewart 1967; Stewart and Stewart 1970, 1971; Field 1972). Identification

of plant fragments is usually facilitated by the use of reference slides which may be prepared in a similar manner, by physical maceration, bacterial degradation or by simulated digestion, of probable or known food items (Fitzgerald and Waddington 1979; Putman 1984). Identified plant fragments are usually quantified by frequency of occurrence (e.g. Stewart and Stewart 1970, 1971; Anthony and Smith 1974, 1977; Owaga 1977; Hosey 1981), using a grid or point quadrat technique (e.g. Chamrad and Box 1964), by area measurements (e.g. Stewart 1967; Seber and Pemberton 1979; Korfhage et al. 1980) or by volume or mass estimates based on point analysis (e.g. Chamrad and Box 1964; Johnson and Hansen 1977).

An alternative means of quantifying herbivore diets from faeces involves the microhistological technique which was first described by Baumgartner and Martin (1939) and later refined by Dusi (1947) both cited in Holechek et al. (1982a), and Sparks and Malechek (1968). Using the table developed by Fracker and Brischle (1944), cited in Sparks and Malechek (1968), frequency of occurrence for each species is converted to density. This permits diet evaluation on a dry mass composition basis, since Sparks and Malechek (1968) found that dry mass percentages could be predicted directly from relative density. (The mathematical rationale for converting frequency to density is discussed by Johnson (1982)). Other studies conducted by Vavra and Holechek (1980), Johnson and Pearson (1981), Holechek and Gross (1982a) and Holechek et al. (1982b) have confirmed that the relationship reported by Sparks and Malechek (1968) is generally true with a few exceptions. However, a 1:1 relationship between relative density and relative percent composition by mass does not exist for all plant species (Westoby et al. 1976; Havstad and Donart 1978; Holechek 1982). Studies by Havstad and Donart (1978) and Holechek (1982) showed that ratios of identifiable to non-identifiable fragments and ratios between grasses, forbs and shrubs were not equal to one. Results from these studies, together with those of Westoby et al. (1976), Vavra and Holechek (1980), Holechek and Gross ((1982a) and Holechek et al. (1982b), indicate that hand-compounded diets should be

used in all studies involving microhistological analysis to test the assumption of a 1:1 ratio between actual and estimated diet percent by mass composition. Regression analysis can be used for correction if certain species do not exhibit this ratio (Vavra and HolecheK 1980). HolecheK and Vavra (1981) have further shown that at least 20 frequency observations should be recorded per slide in order to maintain repeatability between slides, but that an unacceptably large number of slides (up to 156) would be required for adequate precision in the estimation of plants that comprise less than 20% by mass in the faecal sample. These authors concluded that when five or fewer slides are examined, (as in SparKs and MalecheK (1968)), data concerning each species contributing less than 20% by mass are highly imprecise and therefore no conclusion should be drawn regarding the relative proportions of these species in the diet. Despite these serious limitations, and the fact that certain procedures may enhance the accuracy of the microhistological technique (Vavra and HolecheK 1980; HolecheK and Gross 1982b), the method of SparKs and MalecheK (1968) has been applied in an unaltered form, to a variety of studies and currently is probably the most popular means of determining herbivore diets from faecal analysis (e.g. Todd and Hansen 1973; Dearden et al. 1975; Todd 1975; Hansen and ClarK 1977; Kessler et al. 1981; Tilton and Willard 1981; Wydeven and Dahlgren 1982; Adams and Bailey 1983; Campbell and Johnson 1983; Rowland et al. 1983).

The relative merits and disadvantages of faecal analysis largely depend on the intensity of the investigation, the species of herbivore being studied, the nature of its diet and the diversity of plants available for food. For example, food items such as flowers, tubers or acorns would be unidentifiable in faecal samples, while a highly diverse diet would render the technique more time consuming and subject to more errors in identification (Anthony and Smith 1974). Consequently, major disadvantages of faecal analysis stated in some studies may be considered as minor or ignored by other biologists (e.g. Adams and Bailey 1983) with the result that anyone contemplating faecal analysis as a means

of determining herbivore diet is faced with a rather bewildering, and often conflicting, volume of literature.

Various advantages of faecal analysis have been discussed by Ward (1970), Anthony and Smith (1974), Scotcher (1979), Holechek et al. (1982a) and others. Advantages of faecal analysis are:

a) It permits practically unlimited sampling, with minimum disturbance, under entirely natural conditions (Zyznar and Urness 1969; Stewart and Stewart 1970; Todd and Hansen 1973).

b) It has particular value where animals range over mixed communities (Holechek et al. 1982a).

c) It may be the only feasible procedure to use when studying secretive and/or endangered species (Anthony and Smith 1974; Owaga 1977; Smith and Shandruk 1979).

d) It can be used to compare the diets of two or more animals utilizing the same area at the same time (e.g. Stewart and Stewart 1971; Hansen and Clark 1977; Campbell and Johnson 1983; McInnis et al. 1983; Leslie et al. 1984).

e) Actual sampling requires very little equipment and material is easily stored (Fitzgerald and Waddington 1979; Holechek et al. 1982a).

However, faecal analysis also has numerous important disadvantages which have been discussed by Ward (1970), Scotcher (1979), Smith and Shandruk (1979), Vavra and Holechek (1980), Holechek et al. (1982a) and others. These include:

a) Collection should be restricted to fresh material. This is best obtained by collecting faeces from observed animals, which will eliminate mistakes regarding the age of the material and ensure that destruction of plant parts by insects, bacteria and fungi does not occur (Ward 1970).

b) It is not always possible to distinguish between the faecal pellets of different herbivore species when they simultaneously occupy the same habitats. This problem may be solved by confining collections to those from observed defaecating animals (Wilson 1976; Anthony and Smith 1977; Tilton and Willard 1981). Alternatively, several studies have indicated that pH analysis may be used to differentiate between animals with similar faeces (e.g. Howard 1967; Nagy and Gilbert 1968; Howard and DeLorenzo 1974; Krausman et al. 1974). However, more recent work has shown serious limitations in this procedure. Hansen (1978) found that faecal pH values of any herbivore may vary from area to area and with time. MacCracken (1980) and Rollins et al. (1984) also found that faecal pH values may change significantly as the faeces age. Consequently, because the time that has elapsed between defaecation and collection is not normally known in field studies, conclusions regarding the origin of the material may be erroneous. The utility of this technique is further restricted by recent findings which have shown that different herbivore species with similar diets have similar faecal pH values (Hansen 1968; Peek and Keay 1979; MacCracken 1980; Beasom et al. 1982a; Rollins et al. 1984).

c) Accuracy is often a major problem because forage species passed in the faeces are often not in proportion to those that are consumed (e.g. Storr 1961, Slater and Jones 1971, Dunnett et al. 1973 all cited in Wydeven and Dahlgren 1982; Stewart and Stewart 1971; Jackson 1980). This is primarily due to differential digestibility of different plant species (e.g. Talbot 1962; Stewart 1967; Owaga 1977; Fitzgerald and Waddington 1979; Hosey 1981); alternatively altered proportions may result from methods of preparing the material (Fitzgerald and Waddington 1979; see below). Differences in digestibility coefficients are most pronounced when young, actively growing plants are in the forage, because these are highly digestible and have the greatest variation among species (Tilton and Willard 1981), although Holechek et al. (1982b) found that the stage of plant maturity had little influence on the results of microhistological analysis in their study. Several studies (e.g. Dearden et al. 1975;

Pulliam 1978, cited in Kessler et al. 1981; Vavra and Holechek 1980; Leslie et al. 1984) have suggested that the problem of differential digestibility may be allayed by the application of correction factors. However, the use of such correction factors assumes that digestion rates are essentially constant among individual animals of the same species and remain constant for each species even as diet composition changes. Numerous studies, reviewed by Gill et al. (1983) and Putman (1984) invalidate these assumptions.

d) Many plant species are difficult to separate at the species level and sometimes at the genus level, while some species many become unidentifiable in the faeces (Zyznar and Urness 1969; Slater and Jones 1971 cited in Holechek et al. 1982a; Fitzgerald and Waddington 1979; Monro 1982; Putman 1984). Kok (1968) cited in Hofmeyr (1970) found that intraspecific differences may exist in the epidermis of the same leaf blade, including differences between the abaxial and adaxial surfaces, and between leaves on the same plant; such variability may further limit the accuracy of identification.

e) Procedures for sample collection may bias the results (Monro 1982), and unless the observer collects faeces from individual animals, sex and age data cannot be determined (Wilson 1976). Sampling errors may also occur during preparation of the faecal material, e.g. by washing the material through one or more sieves to remove the smaller particles (Monro 1982). Vavra and Holechek (1980) found that some plant species may be destroyed during slide preparation.

f) Plant identification is tedious and time consuming while considerable equipment and labour are needed for actual analysis (Fitzgerald and Waddington 1979). As a result, the technique is expensive (e.g. the cost of analysing each faecal sample from bighorn sheep in Idaho averaged $100,00 (Wilson 1976)). Furthermore, an extensive reference plant collection is required, the preparation of which can be very time consuming or impractical (Fitzgerald and Waddington 1979). Because the abaxial and adaxial surfaces of leaves

usually display different cuticular characteristics, it is often necessary to prepare reference slides from both surfaces (Hofmeyr 1970; Anthony and Smith 1977). An additional problem associated with the procedure is that a considerable amount of time may be needed to train technicians (Ward 1970) and even when trained, there may be considerable variation in the accuracy between technicians (Holechek et al. 1982b). Consequently, Holechek and Gross (1982a) recommended that all technicians using the microhistological technique regularly check their accuracy with hand-compounded diets, and that observers should be replicated when quantifying herbivore diets (Holechek et al. 1982b).

g) Fragmentation may differ between plant species during digestion or slide preparations so that the relative proportion of species in the faeces differs from those consumed (e.g. Stewart 1967; Sneva and Vavra 1978 cited in Kessler et al. 1981; Smith and Shandruk 1979; Putman 1984). Although differential fragmentation may not occur in all herbivore faeces (e.g. Todd and Hansen 1973), milling faecal material to a fairly uniform size (e.g. Smith and Shandruk 1979; Easterbee 1981 cited in Putman 1984; Johnson et al. 1983) or measurements of fragment area (e.g. Stewart 1967; Seber and Pemberton 1979) may alleviate errors when differential fragmentation is a problem. Neither method is ideal however, milling may enhance difficulties associated with identification (Smith and Shandruk 1979; Monro 1982) while area measurements are extremely time consuming and the results may still remain inaccurate (Hofmeyr 1970; Stewart and Stewart 1971; Smith and Shandruk 1979).

h) The evaluation of preference indices is usually not possible because the precise location of where the food was taken, and hence what was available, can rarely be determined. Food retention in the herbivore tract may vary from several hours to 10 days (Ward 1970) and is usually longer for coarse, fibrous or woody particles such as stems (e.g. Cowan et al. 1970 cited in Short 1975; Mautz and Petrides 1971; Jackson 1977; Sinclair 1977; Dunham 1980;

Demment 1982). Therefore in highly mobile species, or where there is a mosaic of small, diverse habitats, relating the presence of plant species in the faeces to the availability of these plants where the faeces were found may well result in highly erroneous conclusion regarding food preferences (Wilson 1976). This limitation has not always been appreciated in wildlife studies (e.g. Adams and Bailey 1983) while Stewart (1967), Stewart and Stewart (1970, 1971) and Owaga (1977) attempted to overcome the problem by monitoring the movements and locations of their study animals for several days prior to faecal collections.

These disadvantages indicate that accuracy is probably the greatest problem associated with faecal analysis. Several studies have further evaluated the accuracy of the technique by comparing results with those obtained from alternative means. Vavra et al. (1978) found that during the growing season faecal analysis tended to underestimate forbs and overestimate grasses when compared to oesophageal fistula sampling. McInnis (1977) cited in Holechek et al. (1982a) obtained similar results from sheep fed known diets, while Smith and Shandruk (1979) found that faeces contained fewer plant species than rumen contents from deer and that forbs were underestimated in faeces of deer fed known diets. Other studies showing lack of agreement between known diets or rumen contents and those determined by faecal analysis include Storr (1961) cited in Holechek et al. (1982a), Stewart (1967), Zyznar and Urness (1969), Anthony and Smith (1974); Westoby et al. (1976); Kessler et al. (1981), Wydeven and Dahlgren (1982) and Gill et al. (1983). When such comparisons are made from wild animals however, their validity is based on the assumption that the subjects had a reasonably consistent diet and thus results would be unaffected by throughput time (Stewart 1967; Anthony and Smith 1974). Putman (1984) provides a means of testing this assumption in such instances. As stated earlier, conclusions regarding the validity of faecal analysis as a means of determining herbivore diets are at variance. The accuracy of the microhistological technique has been tested and found acceptable by a number of authors (e.g. Hansen et al. 1973;

Todd and Hansen 1973; Dearden et al. 1975; Reynolds et al. 1978; Holechek et al. 1982a, 1982b; Wydeven and Dahlgren 1982; Johnson et al. 1983). Others have concluded that faecal analysis can, at best, only provide an approximate indication of dietary composition and is better suited to providing qualitative rather than quantitative data (Ward 1970; Vavra et al. 1978; Smith and Shandruk 1979; Kessler et al. 1981).

Smith and Shandruk (1979) concluded that the claims for accuracy of the faecal analysis technique made by some investigators are overstated. As pointed out by these authors, the widely differing preparation procedures described in the literature are evidence of the dissatisfaction with previous techniques, and it would be particularly informative to determine how results might be influenced by the differing preparation methodologies that have been proposed. Johnson and Pearson (1981) stated that "microscope analysis of botanical composition is as much an art as it is a science". Gill et al. (1983) totally agreed with this statement and suggested that the faecal analysis techniques be used with caution even to identify forage classes in deer diets, while numerous biologists consider the problems and errors of differential digestibility and fragmentation to be so great that the technique becomes worthless (see Putman 1984).

6.1.1.4 Stomach analysis

The determination of wild animal diets by examining digestive tract contents is a technique that has been employed by biologists for well over a century (Medin 1970). Many variations in data collection and analysis have been developed during this time. Because herbivores usually contain a large volume of ingesta in their stomachs or rumens, detailed analyses are usually confined to a smaller, representative subsample that is removed after thorough mixing. Initial separation of plant parts and species is

usually achieved by washing the sample over a series of sieves (e.g. Chamrad and Box 1964; Medin 1970; McCaffery et al. 1974; Puglisi et al. 1978), or by selecting only those plants that have recently been consumed (Talbot 1962). It has always been questionable what should be done with the mass of finer and usually unidentifiable fragments (Ward 1970). Usually this material is discarded, but some authors have determined its mass or volume (e.g. Bergerud and Russell 1964; Leader-Williams et al. 1981) and the proportions of its constituent items may be estimated visually (e.g. Korschgen 1962). Considerable controversy surrounds the use of different sieve mesh sizes. Courtright (1959) cited in Medin (1970) criticized estimation of ruminant food habits when restricted to the larger and easily identifiable fragments. He found that proportional composition of caribou rumen materials trapped on 11 different sieve sizes varied appreciably in relation to different plant groups, and that the composition of large identifiable material was not comparable with that of smaller particles. Bergerud and Russell (1964) found similar results in their caribou samples, which they ascribed to the differential digestion of various forage items. Using sieve meshes ranging from 0,4 to 2,0 mm in size, these authors were unable to identify more than 20% of the plant fragments in their samples, while Coblentz (1970) using a fine "Kitchen strainer" could only identify approximately 8% by volume of the total rumen contents of deer. Scotter (1967) cited in Ward (1970) also found that caribou rumen data obtained from any one of three mesh sizes could be inaccurate and misleading, and consequently combined data from all three sieves for each sample. While these findings are frequently cited examples of the effect of sieve mesh size on diet estimation, it should be noted that the food habits of caribou are not similar to those of other ruminants (Puglisi et al. 1978). In another study, based predominantly on grazers, Owaga (1978) found some significant differences in the results obtained from grass parts and forbs trapped on sieves with mesh sizes of 2 mm and 1 mm. However, she concluded that for three of the five herbivores examined, use could be made of the larger sieve "without much loss in

accuracy", while the mean of the two sieve samples was recommended for the remaining herbivores. In contrast, Dirschl (1962) found little difference in the composition of antelope rumen contents remaining on three mesh sizes ranging from 2,8 to 5,6 mm and therefore recommended the use of the largest sieve. This recommendation was adopted by Mitchell and Smoliak (1971). Harlow and Hooper (1971) cited in Puglisi et al. (1978) reported that 95% of the plant species in white-tailed deer rumen contents could be identified using sieve sizes of 9,5 mm, 6,35 mm, and 5,66 mm. Puglisi et al. (1978) used the same size sieves and found that little material remained on the 5,66 mm sieve; consequently they recommended the use of a 6,35 mm sieve. McCaffery et al. (1974) ignored the fragments on smaller sieves if they appeared to be of similar composition to those on a 6,35 mm sieve. While these conclusions may initially appear to be of academic interest, they have direct practical application. The manual separation and identification of food particles trapped on a sieve is tedious, and the time required for separation increases rapidly with decreasing particle size (Dirschl 1962). Therefore, if quantitative analysis can be restricted to relatively large plant fragments without loss of accuracy, this would result in a considerable saving of time. Several authors have consequently proposed or used extensive sampling (to reduce variability) rather than intensive analysis (e.g. Puglisi et al. 1978; Jackson 1977; Leader-Williams et al. 1981; Monro 1982). However, if sample size is limiting, sampling errors are increased with the use of sieves while identification errors increase if sieves are not used; thus some error is unavoidable (Monro 1982).

An alternative means of dealing with differential fragment size involves milling the ingested food particles and examining these microscopically (e.g. Malechek 1966 cited in Ward 1970; Sparks 1968; Westoby et al. 1976). While this procedure may result in fragments of more uniform size, the milled material is still sieved and therefore subject to sampling errors, while additional identification errors may result from the reduction in particle size (Monro 1982).

Once initial separation is completed, various quantitative expressions may be used to appraise and describe dietary consumption. Unidentifiable fragments (of a predetermined size) are usually included in such appraisals, although Short (1971) expressed individual food items as percentages of the total identified sample, which averaged about six percent of the total rumen contents. Such a procedure would greatly bias comparisons between two or more herbivore species with dissimilar diets. In microanalyses, the composition of the diet is usually expressed as frequency of occurrence (e.g. Stewart 1971; Field 1972; Todd and Hansen 1973; Owaga 1977; Dunham 1980) or relative density using the method of Sparks and Malechek (1968) as outlined above (e.g. Dearden et al. 1975; Kie et al. 1980; Kessler et al. 1981; Wydeven and Dahlgren 1982; McInnis et al. 1983). In macroanalyses, tabulation of food item numbers, tabulations of frequency of food item occurrences, and estimates of food items by volume or mass measurements are most commonly used (Medin 1970). Tabulation of food items alone has been criticized as not being a sufficiently comprehensive indication of diet (McAtee 1912 cited in Medin 1970). Certain foods, such as fruit pulp, sap and fragmented vegetative matter cannot be assessed numerically nor can allowance be made for different sizes of food items. A record of food items eaten, often in conjunction with some arbitrary assessment of use or importance, is nevertheless a common means of presenting diet data (e.g. Hitchins 1968; Pooley 1968; Kufeld et al. 1973; Anderson and Pooley 1977). The frequency of occurrence of food items provides a much more important interpretive index (Medin 1970), and although in some studies it has been used exclusively (e.g. Owaga 1975; Dominguez 1976; Irby 1977), it is more commonly associated with other descriptive expressions.

Volume is probably the most consistently applied descriptive statistic used in diet analyses, and may be estimated visually (e.g. Anderson et al. 1965; Korschgen et al. 1980), or measured directly by water displacement in graduated cylinders (Martin et al. 1946). When direct volumetric measurement is involved, two alternative methods

of summarizing data are available. In the "aggregate percentage" method the volumetric percentage of the ith food item is summed and divided by the number of stomachs examined, while in the "aggregate volume" method, the actual volume of the ith species is summed and divided by the total volume of food examined (Martin et al. 1946). Thus the aggregate percentage method gives equal weight to each animal in the analysis while the aggregate volume method gives equal weight to each unit of food consumed by any animal. Various merits and disadvantages of these two methods are discussed by Martin et al. (1946) and Swanson et al. (1974). Only the aggregate percentage method can be used when volumes are estimated visually. Numerous authors have favoured the aggregate percentage method even when volumes of food have been measured from the digestive tracts of birds and herbivores and omnivorous mammals (e.g. Dirschl 1962; Martinka 1968; Allen 1968; Bayless 1969; Nellis and Ross 1969; Mitchell and Smoliak 1971; Anthony and Smith 1974; Swanson et al. 1974; Landers et al. 1979) while other authors have preferred to summarize their data using the aggregate volume method (e.g. Carpenter 1971; McCaffery et al. 1974; Hubert et al. 1980; Korschgen et al. 1980) and yet others have presented results using both techniques (e.g. Ward 1964; Maehr and Brady 1984). Despite the recommendation of Martin et al. (1946) that authors should clearly indicate which of the two methods are used, many authors have omitted such details (e.g. Korschgen 1962; Boag 1963; Bergerud and Russell 1964; Webster 1964; Coblentz 1970; Robel and Watt 1970; Bergerud 1972; Harlow et al. 1975; Jackson 1977, 1980; Puglisi et al. 1978; Kessler et al. 1981; Staines et al. 1982). Such omissions limit the extent to which meaningful comparisons of diet may be made between populations or between years for the same populations. The expression "percent volume" adds further confusion when it is used in the point analysis method (see below) to indicate the percentage of sample points that contact the plant species in question (e.g. Chamrad and Box 1964, 1968; Drawe 1968; McCaffery et al. 1974).

In contrast, most published accounts of diet assessment

based on dry mass data detail the methods used to determine such values. The dry mass of each forage species is usually expressed as a percentage of the total dry matter examined (e.g. Nixon et al. 1970; Segelquist et al. 1972; Hall-Martin 1974a; Skinner and Telfer 1974; Johnson et al. 1978; Wood and Roark 1980; Kaluzinski 1982) and is therefore the mass equivalent of the aggregate volume method of Martin et al. (1946). Short et al. (1969a) adopted a similar method with the exception that only identified material was considered in the final analysis. While assessment by mass has been considered a more laborious yet refined method of presenting food-habits data (Medin 1970), Ward (1970) has pointed out that because digestion starts as soon as the plant is eaten, any readily digested materials are immediately dissolved. Since these are usually liquids or fast-dissolving substances that do not account for a large volume but are heavy, their rapid disappearance should be considered before commencing with the added work of dry mass measurements (Ward 1970). Estimates of dry mass are however used when dealing with aspects related to diet quality, digestibility and nutritional requirements (e.g. Short et al. 1969a, 1969b; Hall-Martin and Basson 1975; Hoppe et al. 1977; Staines and Crisp 1978; Wood and Roark 1980).

Another means of assessing the dietary composition of stomach samples is the point frame method. This was described by Chamrad and Box (1964) and is an adaptation of the point quadrat, which is often used to sample vegetation. Sieved fragments are placed in a tray and those touched by a series of pins are identified. The technique has been used to determine percent composition based on frequency (e.g. Coblentz 1970; Robel and Watt 1970; Owaga 1977, 1978) or "quantitative percentage" (Jackson 1977, 1980), but since Chamrad and Box (1964) concluded that "percentage volume estimates may be taken directly from hits in most cases", biologists commonly have expressed their results as volumetric composition (e.g. Chamrad and Box 1968; Drawe 1968; Boeker et al. 1972; McCaffery et al. 1974). Staines et al. (1982) refined the method in their study, where fragment counts were converted to volumes using regressions obtained

homogeneous mixtures would therefore result from each rumen sample, and each would require a separate point-analysis measurement. These recommendations are considered to be of dubious value. The rejection of "unusually large items" may result in serious omissions concerning principal food items while, as Robel and Watt (1970) point out, multiple point-analysis measurements of each rumen sample would tend to nullify any large time-saving advantage the technique may offer.

Several authors reviewed in Medin (1970) have pointed out the limitations of any single quantitative description of dietary composition determined by stomach analysis, and it is clearly desirable to use two or more complementary expressions whenever possible. Anderson et al. (1965) adopted such an approach, using an "adjusted ratio" which was the product of the mean volume (aggregate percentage) and frequency (decimal value) for each major species. A similar "relative importance factor" was calculated for principal foods by McCaffery et al. (1974) also involving aggregate volumes but using percent occurrence. Unless ranked, these indices are not easy to interpret, but Jackson (1980) provided a refined version by expressing the "importance factor" (quantitative percentage x percentage occurrence) for each species as a percentage of the total importance factors for all species.

Although many of the inherent biases of faecal analysis also apply to stomach analysis, the magnitude of these may be appreciably lower when sampling from the stomach due to only partial digestion/assimilation. Further, difficulties in identification of partially digested food items (e.g. Anderson et al. 1965) may be alleviated by collecting animals that are actively feeding (e.g. Swanson and Bartonek 1970), which, when possible, provides the location of consumption that cannot otherwise be determined. In addition, volumetric or gravimetric measurements reduce the errors associated with differential fragmentation caused by mastication, rumenation and/or digestion. One of the most frequently cited disadvantages of stomach analysis is that it involves

sacrifice of animals (e.g. Smith and Shandruk 1979; Kessler et al. 1981; McInnis et al. 1983) and therefore is restricted primarily to common species with abundant populations. However, numerous feeding studies have been based on material collected, at least in part, from animals that were killed for reasons other than diet collection, e.g. from hunting (Korschgen 1962; Bergerud and Russell 1964; Short et al. 1969a; Nixon et al. 1970; Mitchell and Smoliak 1971; Boeker et al. 1972; Harlow et al. 1975; Johnson et al. 1978; Landers et al. 1979) as a result of road accidents (Martinka 1968; Robel and Watt 1970; McCaffery et al. 1974; Skinner and Telfer 1974; Korschgen et al. 1980) or from culling operations or natural mortalities (Hall-Martin 1974a; Jackson 1977, 1980).

Trocar samples may be collected from immobilized large ungulates when rumen contents are required but killing of the animals is not warranted (e.g. Follis and Spillett 1972; Wilson et al. 1977). Sampling errors may however result from layering of the rumen contents, and because of other complications associated with parasites, disease and overdosing, Holechek et al. (1982a) recommend that the technique is not used on rare or endangered species. The utility of the method may therefore be questionable, since the financial costs associated with such a procedure are likely to preclude its adoption on more common species when easier and cheaper methods are readily available.

Because rumen samples relate mainly to the food eaten during the previous 48 hours (Mitchell et al. 1977), possibly the major disadvantage of stomach analysis is one of collecting a representative number of samples (e.g. Hanson and Graybill 1956; Anderson et al. 1965; Anthony and Smith 1974; Monro 1982). Since animals are usually killed, samples are non-repeatable, while animals may feed on totally different plants at different times of the day (Mitchell et al. 1977) or show considerable variations in their diets over a period of a few days (Medin 1970). Animals also vary in the diet they select from different locations, seasons, and even years (Boag 1963). Differences in diet related to age

(Boag 1963; Pendergast and Boag 1970; Wilson 1976; Leader-Williams et al. 1981) and sex (Wilson 1976; Dunham 1980; Korschgen et al. 1980; Staines et al. 1982), have been reported and perhaps even less apparent, diets may vary among individuals when the same choices of food are on offer (e.g. Duvendeck 1962; Marten 1978). Intensified sampling is necessary to reduce the variability from all of these sources, yet this may not always be possible. Nevertheless, the examination of stomach contents does provide estimates of the kinds of food taken by animals and can indicate the relative proportions in which food items are consumed (Medin 1970; Holechek et al. 1982a). Consequently it is generally accepted as being more quantitatively representative than faecal analysis (Puglisi et al. 1978; Smith and Shandruk 1979).

6.1.1.5 Fistula techniques

Although oesophageal and rumen fistula techniques have considerable advantages over the sampling methods described above, (McInnis 1976 cited in Kessler et al. 1981; Holechek et al. 1982a), fistulation is rarely extended to wildlife species because tractable animals amenable to frequent handling are essential (Vavra et al. 1978). The technique therefore necessitates the use of tame animals (e.g. Nge'the and Box 1976; Staines 1976; Usenik et al. 1977; Staines and Crisp 1978; Wickstrom et al. 1984) whose feeding preferences have not been influenced or altered by taming (Talbot 1972).

The development, use and relative merits and disadvantages of oesophageal and rumen fistula techniques have been reviewed by van Dyne and Torrell (1964) and Rice (1970). The oesophageal fistula is generally preferred over the rumen fistula because rumen evacuation subjects animals to abnormal physiological conditions, is limited to large animals, and is more laborious (Rice 1970). Further, oesophageal fistula samples have been shown to be more representative of known diets than rumen samples (Holechek et

al. 1982a). Problems associated with oesophageal fistulation include surgery (Rice 1970) and intensive post-surgical care (Usenik et al. 1977); incomplete collections (Lesperence et al. 1974 cited in Holechek et al. 1982a); the foraging behaviour of fistulated animals may differ from that of intact animals (Engels and Malan 1973 cited in Vavra et al. 1978); fistulated animals can only be fed for short period of time (van Dyne and Torrell 1964); contamination by saliva and rumen contents (Rice 1970); and high costs and low sampling precision (Holechek et al. 1982a).

Methods of determining the botanical composition of fistula samples may be either macroanalytical (e.g. visual appraisal, manual separation with volume or mass analysis) or microhistological, all of which have been detailed earlier (see faecal and rumen analysis).

6.1.1.6 Food preference and quality

The techniques detailed above can provide a wealth of data regarding what forage species are eaten as well as where and when these plant are taken. The most important species are obviously those that are eaten in the greatest quantities, i.e. those that form the largest percentages of food items in the diet. Petrides (1975) proposed the term "principal foods" for such species. Knowledge of whether these foods have been eaten in proportion to their availability, or whether these foods have been actively selected by the foraging herbivore is often of considerable importance to the wildlife manager. For example, large scale plantings of preferred forage species may be recommended to sustain or increase herbivore populations (e.g. Yoakum and Dasmann 1969) or to reduce browsing damage to commercial species (Campbell and Evans 1975a, 1978), while the rapid utilization and disappearance of preferred species is often indicative of overpopulation (Halls and Crawford 1960; Klein 1962, 1970, 1981; Kie et al. 1980).

Unfortunately, numerous authors have used the terms

"preference" or "preferred foods" without any consideration of their relative availability in the environment (e.g. Talbot 1962; Martinka 1968; Nellis and Ross 1969; Bergerud and Nolan 1970; Hofmeyr 1970; Jungius 1971a; Bergerud 1972; Bergerud and Russell 1974; Rodgers 1976; Wilson et al. 1977). The use of these terms is incorrect and should be replaced by "principal foods" if one accepts Petrides (1975) definitions that a preferred food species is "one which is proportionately more frequent in the diet of an animal than it is in the available environment" and that food preference is "the extent to which food is consumed in relation to its availability".

Preference indices are commonly used to determine if actual selection occurs, and these are frequently calculated as the ratio of the estimated percentage of a food item in an animal's diet divided by estimated percentage of that food available in the habitat where the animals feeds. Values of this index exceeding one are considered to indicate preference, those values less than one indicate rejection, while those approximately one are neither preferred or avoided but are eaten in proportion to their abundance in the field (Medin 1970; Ward 1970; Petrides 1975; Hobbs and Bowden 1982). Methods of estimating utilization and availability have varied considerably between authors. Korschgen et al. (1980) considered that the frequent intake and heavy utilization of a few plants among the hundreds that were available to deer were indicative of preferences, and thus where deer populations were within the carrying capacity of the habitat, utilization was equivalent to preference. Several biologists have based utilization on frequency of occurrence while scales of abundance have been used to estimate availability (e.g. Stewart 1971; Stewart and Stewart 1970, 1971; Kohn and Mooty 1971). Chamrad and Box (1968) and Drawe (1968) used a similar index except that utilization (their so-called "preference value") was the product of percentage frequency and percentage volume for each species eaten. A similar estimate of use was made by Krausman (1978) who determined availability from the product of percent frequency and percent density of each species in

the field. Peek et al. (1976) devised an "importance value" by summarizing frequency of occurrence for each species within all feeding sites, plus the aggregate percentage relative abundance for each species, plus the aggregate percentage utilization and dividing by 3. Other indices have included estimated volume and percent frequency of occurrence or percent dry mass for utilization and availability respectively (Boeker et al. 1972; Mitchell and Smoliak 1971) or frequency of occurrence (utilization) and percent cover (Hjeljord 1973; Adams and Bailey 1983; Wydeven and Dahlgren 1983), percent fresh mass (Crouch 1968), or percent dry mass (e.g. Segelquist and Green 1968; Segelquist et al. 1972; Owaga 1975, 1977; Schwartz et al. 1976; Dunham 1980) as estimates of availability. It can be seen that all of these authors have used differing means of estimating utilization compared to availability. Medin (1970) suggested that greater precision may be achieved by using comparable methods to estimate use and availability. Simple examples of such an approach using percent frequency of occurrence have been detailed by Field (1970, 1976), Wetzel et al. (1975), Henry (1978), Scotcher et al. (1978), Leuthold (1979), McNicol and Gilbert (1980), and Kossak (1983). In a study comparing two different methods, Telfer (1972) found that biomass values gave a more accurate estimate of preference than a rating based on the relative number of stems browsed and the relative number available. Dry mass values of utilization and availability have also been used in a number of captive animal feeding studies (e.g. Schwartz et al. 1980; Papageorgiou et al. 1981) as well as in numerous studies of wild populations (e.g. Collins et al. 1978; Deschamp et al. 1979; Blair and Brunett 1980; Stormer and Bauer 1980; Szukiel 1981; Collins and Urness 1983). Finally, preference indices need not be confined to individual species but may be used to determine preference ratings for any aspect of the diet, including plant parts, which may be of more significance than the species eaten (Medin 1970).

While a detailed discussion on the techniques used to assess forage availability is beyond the scope of this review, (but see Bobek and Dzieciolowski (1972), Bobek and

Bergstrom (1978), Bobek et al. (1979) and Oldemeyer and Regelin (1980) for methods of browse biomass and shrub density estimation in forests), such estimates have in the past been limited in scope and intensity (Medin 1970). Even when attempts have been made to obtain more precise estimates of availability, these may suffer from a number of limitations that are not commonly stressed in the literature. For example, surveying transects or quadrats and counting twigs can give a very different estimate of availability than would be obtained if researchers encountered foods in the same way that animals do. The foraging path of an animal may be a nonrandom path through patches of differentially favourable habitats, and for this reason use estimated from rumen or faecal analyses can differ from use estimated from twig counts (Harlow 1979 cited in Nudds 1980). Field's (1970, 1976) method of following a tame animal and noting all the plant species eaten or ignored within a specified distance from the animal's head is therefore considered a better measure of preference than by obtaining availability data from random transects that may not even be visited by the foraging animal (see Loehle and Rittenhouse 1982). Wetzel et al. (1975) adopted a similar technique except that fresh tracks of wild deer were followed and use was assessed from the numbers of browsed species within 1 metre of the track, while availability was determined by counts of stems and twigs of each species in 4 m^2 plots established at regular intervals along the track.

More serious limitations of availability are evident when use is estimated from rumen or faecal samples, since it is rarely possible to determine the precise location where the food was actually taken. Instead, researchers often measure availability at the collection site, yet such a procedure may be meaningless if the herbivore species is highly mobile or inhabits a mosaic of heterogenous habitats. These limitations have been recognised by Sparks (1968), Wilson (1976), and Kuen and Bubenik (1977).

In conclusion, preference ratings should be interpreted with caution because they may depend on the methods and

season of data collection and on the statistic used to quantify preference (Nudds 1980). Telfer (1972) demonstrated that serious inaccuracies resulted from different methods of preference estimation at the same sites, yet preference indices continue to be calculated as if animal diets and food availability are measured without error. Further, it is often suggested that one food is preferred over another because it has a higher preference index, yet, as Hobbs and Bowden (1982) point out, for these inferences to be statistically valid, it is necessary to estimate the error associated with each preference index value. These authors provide a method of calculating confidence intervals on simple ratio preference indices and demonstrate, together with Loehle and Rittenhouse (1982), the danger of inferences based solely on estimates, particularly for species which occur infrequently in the diet or are rare in the habitat. Consequently, unless care is taken to obtain precise use and availability data, the preference index is virtually meaningless, and estimates of preference unaccompanied by confidence intervals can be grossly misleading; their use should therefore be avoided (Hobbs and Bowden 1982).

Assuming that forage preferences have been accurately assessed, these provide a starting point from which to undertake more intensive studies concerning reasons why certain species are selected or avoided. This proves to be much more difficult and complex than determining what species are eaten and where and when they are taken (Medin 1970; Putman 1984). Selection is not just a case of one species being preferred more than another, but may depend partly on what else is available. For example, deer may eat relatively small proportions of Artemisia tridentata when it is fed alone, but larger amounts if highly preferred species are also available (Dietz et al. 1962 cited in Klein 1970; Carpenter et al. 1979). Selection for a single plant species may also vary between individual herbivores or between years, and may be influenced by management practices (Mitchell et al. 1977). Holloway (1967) cited in Mitchell et al. (1977) showed that red deer browsed more heavily on replanted nursery-grown seedlings of Scots pine (Pinus sylvestris) than

on naturally-regenerating ones, and browsing severity increased after fertilising the seedlings. Other effects of fertilization are reviewed by Duvall (1970) and Hanson and Smith (1970). Burning may also affect the degree of utilization of an area and many herbivores prefer to feed on the subsequent growth because it is more accessible and more nutritious (e.g. Lay 1957; Klein 1970; Taber and Murphy 1971; Bergerud 1971b; Johnson and Landers 1978; Hobbs and Spowart 1984). Silvicultural practices including clearfelling (e.g. Murphy and Ehrenreich 1965; Halls and Alcaniz 1968; Halls and Epps 1969; Duvall 1970; Hanson and Smith 1970; Hooven 1973; Regelin et al. 1974; Davis 1977; Regelin and Wallmo 1978; Lyon and Jensen 1980; Stransky and Halls 1980; Monthey 1984), thinning (e.g. Blair 1967; Young et al. 1967; Behrend and Patric 1969; Crawford 1971; Halls and Alcaniz 1972; Halls 1973a, 1973b; Blair and Feduccia 1977; Blair and Brunett 1980; Conroy et al. 1982) and cleaning (e.g. Della-Bianca and Johnson 1965; Crawford and Harrison 1971; Lawrence and Biswell 1972; Wolters and Schmidtling 1975) may have similar effects in forested areas, although of course increased utilization may be in direct response to increase availability and therefore may not necessarily reflect preferences in these instances. Where utilization of commercial species becomes excessive, attractants in the form of alternative species, supplementary food or substances (e.g. sweeteners, minerals, or trace elements) sprayed onto surrounding vegetation may be used to alleviate damage (Dasmann et al. 1967). More commonly however, repellents are applied in attempts to reduce the palatability of the species being browsed (e.g. Duvall 1970; Campbell and Evans 1977; Lindsey 1977; Caslick and Decker 1977, 1978, 1980; Decker and Sanyal 1983; Harris et al. 1983).

The growth form or habit of a plant may also directly affect its use by an animal. Certain species may be unavailable except when young because of their physiognomy, other plants may be unavailable due to their geographical position, while others may be avoided because of animal-repellent characteristics such as thorns or secondary

plant compounds which are toxic (e.g. Fowler and Richards 1965; Mueggler 1970; Schwartz et al. 1980). It is also probable that preferred species will be selected only when they are present above a certain critical percentage in the vegetation. If their density is too low or they are too widely dispersed, then it may not be profitable for the herbivore to seek them out (Mitchell et al. 1977; Westoby 1978; Nudds 1980). Conversely, animals may gorge themselves on abundant, highly preferred foods. While protein is considered the most important nutrient to the animal, very high protein levels are not only unnecessary but are inefficient for ruminant animals (Dietz 1970). Similarly, large quantities of readily fermentable carbohydrate may be deleterious or fatal to ruminants (Wobeser and Runge 1975).

Plant species may be selected for a variety of different nutritional reasons. A given food item may meet an animal's nutritional requirement for energy but be lacking in mineral content or protein. Therefore, the animal must usually select a diet from several food items of unequal nutritive value that provide an adequate mixture of essential nutrients (Mitchell et al. 1977; Westoby 1978; Vangilder et al. 1982). While numerous animal, plant and environmental factors may influence diet selection (see Heady 1964; Marten 1978; and Hanley 1982), most efforts to explain preferences have centered on diet quality, largely because the intensive management of any ungulate species necessitates a thorough understanding of the benefit these animals derive from each forage species that is selected. It is generally agreed that in the absence of predators, the quantity of available forage governs ungulate population size, whereas forage quality determines the size and performance of the individual (Klein 1968). Consequently, realistic habitat evaluation, based on forage supplies and forage quality, is possible provided that the nutritional requirements of the managed herbivore are known (Wallmo et al. 1977).

High quality forage is generally considered to be highly palatable, has optimum levels of various nutrient components, has a high apparent digestibility, has optimum proportions of

volatile fatty acids, has adequate levels of minerals, vitamins and trace elements, and is efficiently converted into the components necessary for the animal's body (Dietz 1970). Several factors can influence the nutritive quality of plants (e.g. Laycock and Price 1970) and these have been listed by Oelberg (1956) cited in Klein (1970) as a) the stage of the maturity of the vegetation, with highest nutritive quality coinciding with the initiation of growth; b) soil factors; c) climate; d) variations within plant species including differential digestibility, presence of toxic or inhibitory substances and growth rates; e) animal class (i.e. the differential ability of animal species to digest plant material) and f) the conditions of the vegetation (e.g. related to previous land management or animal use altering plant successions).

There are three main ways of assessing forage quality in ruminants. These are:

(i) Using chemical analyses (e.g. proximate, Van Soest and mineral) of the main food species as indices (e.g. Ullrey et al. 1967; Halls and Epps 1969; Segelquist et al. 1972; Smith and Malechek 1974; Urness et al. 1975; Hobbs et al. 1981, 1983; Baker and Hobbs 1982; Bobek et al. 1983).

(ii) Feeding natural foodstuffs to captive animals and measuring in vivo digestibilities using either macrodigestion or microdigestion techniques (e.g. Short 1970, 1975; Short and Epps 1976; Robbins et al. 1975; Mautz et al. 1976; Blair et al. 1977).

(iii) Making estimates from wild herbivores e.g. in vitro digestibility studies (Pearson 1970; Short 1971; Oldemeyer 1974; Radwan and Crouch 1974; Snider and Asplund 1974; Robbins and Moen 1975b; Oldemeyer et al. 1977; Everitt and Gonzalez 1981; Vangilder et al. 1982), chemical indicators in the faeces (Erasmus et al. 1978; Putman and Hemmings 1983 cited in Putman 1984) or the chemical composition of rumen contents (Klein 1962; Hall-Martin and Basson 1975; Harlow et al. 1975; Staines and Crisp 1978; Kie

et al. 1980; Staines et al. 1982).

All of these methods have limitations and biases so that ideally one should be used in conjunction with another (Mitchell et al. 1977). A comparison of chemical analyses may not always be particularly informative in evaluating the nutritional usefulness of browse (Ullrey et al. 1967) largely because of high intraspecific variation resulting from plant part, phenology, vigour and habitat (Hanley 1982), while in vivo digestibility trials are time consuming, expensive and require large amounts of forage (Morris and Kovner 1970; Pearson 1970). The main disadvantages of the in vitro technique are associated with the lack of standardized procedures (Pearson 1970) although as Morris and Kovner (1970) point out, possible differences in a) the behaviour of the innocula donor compared to intact animals and b) the innocula obtained from donor animals compared to those of intact animals feeding in the same habitats, may have been overlooked. In addition, there is considerable evidence to suggest that forage sampled by hand for in vivo and in vitro techniques may differ from that selected by the foraging animal (Bissell 1959 cited in Klein 1962; Boeker et al. 1972; Van de Veen 1979 cited in Putman 1984; also see Gurchinoff and Robinson 1972). As Putman (1984) points out, the mere fact that the sample taken by the human experimenter is available to be plucked, and has not yet been removed by the foraging animal, suggests that it may be of lower quality than that which has already been eaten (see 6.1.2).

6.1.2 Previous Feeding Studies of Bushbuck and Duiker

6.1.2.1 Bushbuck

The bushbuck has invariably been reported as a browser, feeding primarily on the leaves, shoots, flowers, and fruits of a wide variety of trees, shrubs and forbs (Van der Schijff 1959; Brynard and Pienaar 1960; Wilson and Child 1964; Glover et al. 1966 cited in Hofmann and Stewart 1972; Von Gadow 1970; Bainbridge 1973; Jacobsen 1974; Simpson 1974b; von

Breitenbach 1974; Okiria 1980; Kingdon 1982; Smithers 1983). Based on stomach structure, Hofmann and Stewart (1972) classified the bushbuck as a selector of juicy concentrated herbage; specialising in fruit and dicotyledon foliage. Jarman (1974) also considered the bushbuck as a highly selective browser, feeding on plant parts of high nutritional value.

Wilson and Child (1964) presented a species list of 15 plants identified from the rumens of 46 bushbuck shot in Zambia. None of the more detailed bushbuck studies have attempted to quantify the diet of this antelope, except in recording the frequencies with which various species were eaten and their relative abundance in the field (Jacobsen 1974; Simpson 1974b; Okiria 1980; Odendaal 1983). Okiria (1980) also performed chemical analyses on some of the plants eaten by bushbuck. With the exception of Odendaal's (1983) work, all of these studies were conducted in areas of natural vegetation to the north of South Africa. Thus, apart from references to the plant parts of forage classes eaten by bushbuck, these accounts are of little relevance to this study. Wilson and Child (1964), Jacobsen (1974) and Okiria (1980) noted that grass was consumed during most months of the year. Dicotyledons leaves dominated the diet of bushbuck in all of these studies, while Simpson (1974b) and Okiria (1980) found that flowers and seeds/fruits were also readily eaten.

Odendaal's (1983) study was conducted on Forestry land in the southern Cape. A total of 47 food plants were identified to genus, but quantitative analyses were confined to four floristic categories from 16 rumen samples collected in winter. Dicotyledons formed the major portion of the diet (83%) followed by monocotyledons (10%), fleshy fungi (5%) and ferns (1%). The bulk of the dicotyledon foliage eaten was from trees, while forbs were more frequently consumed than shrubs. Thirteen rumen samples were also used for proximate analysis and Odendaal (1983) concluded that bushbuck in that region had a high plane of nutrition during the winter months.

6.1.2.2 Duiker

Hofmann and Stewart (1972) placed the duiker in the same dietary category as bushbuck, and all published accounts indicate that the duiker is essentially a selective browser consuming a wide variety of leaves, shoots, flowers, seeds, fruits and roots from numerous dicotyledons (Van der Schijff 1959; Brynard and Pienaar 1960; Wilson and Clarke 1962; Wilson 1966a; Keymer 1969; Smithers 1971,1983; Mentis 1973a; Zaloumis and Cross 1974; Kingdon 1982). Several of these authors have also noted the inclusion of animal protein in the diet of this antelope, including insects, molluscs, amphibians, birds and small mammals (Wilson and Clarke 1962; Wilson 1966a; Smithers 1971; Zaloumis and Cross 1974; Kingdon 1982). Wilson and Clarke (1962) and Wilson (1966a) each examined nearly 200 duiker rumens, but neither of these authors attempted any quantitative analyses. Smithers (1971) also presented a species list of plants eaten by duiker in Botswana, and all of these authors concluded that duiker consumed very little quantities of grass. Little attention has been paid to the availability of food items listed in these studies, and consequently statements concerning the food preferences of this antelope are largely subjective.

Aspects of duiker digestive physiology, including volatile fatty acid production, have been studied by Boomker (1983).

6.2 METHODS

As detailed in Chapter One, the primary objectives of this aspect of the study were to determine the feeding ecology of bushbuck and duiker in a forest environment, their level of interspecific competition, and the impact that these two species have on current forestry management practices. Initial studies of their feeding strategies revealed that both species were browsers, and the nature of their diets did

not lend itself to faecal analysis (faeces were difficult to detect in the vegetation and dense understory of many of the habitats anyway; see Chapter Nine). Since both species are largely nocturnal, inhabit densely structured vegetation, and are extremely wary at Weza, their diets could not be determined by direct observation. Utilization techniques were also regarded as unsuitable for the determination of diets since plant usage could not be distinguished according to antelope species, while fistula techniques involving tame animals were considered beyond the scope of this study. Rumen analysis was therefore the obvious choice of method, particularly since culled animals were also required for age determination, population structure, growth, reproduction and condition assessment purposes. While rumen analysis could provide detailed data regarding the feeding ecology, level of competition, and extent of utilization of commercial species in relation to other food resources by both bushbuck and duiker, the technique could not provide any means of assessing the extent to which these feeding strategies might affect silviculture. This latter aspect was examined by the use of utilization techniques in areas where one or several commercial species were available.

6.2.1 Rumen Analysis

Rumen contents were obtained from 129 bushbuck and 116 duiker which were randomly culled within the extensive study area between September 1980 and August 1984. Additional rumen contents were sampled from 30 bushbuck and 8 duiker that died from accidental or natural causes within both intensive and extensive areas. For comparative purposes, fresh rumen material was also collected from 58 bushbuck and 25 duiker that were shot on neighbouring farms during the hunting seasons of 1981 to 1984.

Once measured and weighed, each animal was eviscerated and its rumen opened. A sample of approximately 200 ml of rumen material was removed once the entire contents had been

thoroughly mixed by hand, but entire rumen contents were taken from young animals or those with a relatively empty rumen. Samples were then washed gently but thoroughly on a 6,35 mm mesh sieve after it had been established that this size of screen yielded a representative sample of the total diet (see 6.3.1.1). Retained food items were then stored in formal-acetic-alcohol until February 1984 when culling was almost completed. A reference collection of preserved, browsed plants was established during the culling operations and collected plants were identified by the botanist at the Directorate of Forestry, Pietermaritzburg, the Botanical Research Institute and Professor Hilliard at the herbarium, University of Natal. Dried voucher specimens were lodged with both the Directorate of Forestry and the Botanical Research Institute. Plants consumed by bushbuck and duiker were identified by eye or dissecting lens by comparing these to the reference collection. (Browsed species collected in the field but not found in rumen contents are listed in Appendix C.1). Discernible plants not included in the reference collection could often be identified by qualified botanists, and such identifications were facilitated by the author revisiting the site where the animal was culled (which was recorded on the data form for each animal that was shot or found dead in the field) and collecting fresh, growing specimens (see Wilson 1966a). Fungi, grasses, bryophytes, sap and bark were listed under general, rather than specific headings.

Quantitative analysis was accomplished for every identifiable species occurring in each rumen using volumetric determination by water displacement in a series of different sized graduated cylinders. Volumes were measured to the nearest 0,05 ml; plant fragments smaller than this were recorded as present but represented a trace value. The contribution that each species made to the total diet of that animal (or group of animals over a given period of time) was determined by the aggregate volume method (the rational behind this decision is given in 6.3.1.1). The relative proportions of plant parts and forage classes consumed by bushbuck and duiker were also determined by the aggregate

volume method. Categories of plant parts considered were leaves, leaves and stems, stems, fruit, flowers, fungi and grass. The category "leaves and stems" was included since the proportion of foliage to fibre varied enormously, and it could not be ascertained which (if either) was more important in influencing the animal's decision to consume these items. Browse consisted of leaves, leaves and stems and stems. Forage classes noted were trees and shrubs (since most trees browsed by bushbuck and duiker were of shrub height), forbs, (i.e. non-woody dicotyledons, see Hofmann and Stewart (1972)), ferns, grasses and fungi. Unidentified species were included in plant part analyses, but were omitted from forage class assessment as it was impossible to distinguish between trees/shrubs and forbs solely on the basis of leaf, flower or fruit morphology.

The percentage occurrence of each identified species in the diets of bushbuck and duiker were presented as decimal values, and subsequently referred to as the "frequency index". Since neither % volume or % occurrence is considered a particularly meaningful statistic (see 6.1.1.4), a "principal food index" (PFI) was calculated for each species as a product of the % aggregate volume and the frequency index. Even when ranked, these PFI values were difficult to interpret due to the widely diverging indices that were obtained. Consequently, for any given period, PFI values were summated for all species and the percentage that each individual species contributed was calculated, and subsequently referred to as a % PFI value. This procedure is similar to that adopted by Jackson (1980).

Dietary overlap was estimated as the percentage of individual plants common to the diets of both bushbuck and duiker, i.e. the percentage that was identical (Jarman 1971; Hansen and Clark 1977; Anthony and Smith 1977). As Jarman (1971) points out, overlap in this context is essentially a measure of similarity (see Horn 1966) while Oosting (1956) cited by numerous authors (e.g. Hansen and Clark 1977; Campbell and Johnson 1983; Hobbs et al. 1983; Dailey et al. 1984; Thill 1984) refers to this method as Kulcyznski's

similarity index.

The first rumen samples to be identified and measured were re-examined once all rumens had been analysed. This was done to ensure that plants had not been misidentified or omitted during the initial phase of the study when I was inexperienced in rumen analysis and unfamiliar with many of the plants that were consumed. Where omissions or errors in identification had occurred, these were corrected and all corresponding data were revised prior to final dietary assessments. This procedure was continued until five consecutive, re-examined rumen contents did not differ from the original results, and was achieved for both species before 25 rumen samples had been re-evaluated.

Due to time and financial constraints, food quality could not be analysed during this study. The original, washed rumen samples are however housed at the University of Natal and would be available to any interested party for such a study. Plant nomenclature used in this study follows Poynton (1971), Acocks (1975), Coates Palgrave (1977) and Moll (1981).

6.2.2 Utilization of Commercial Species

A total of 4 950 pines, 400 poplars, 100 wattles and 100 camphors were monitored for browsing assessment purposes between December 1980 and November 1982. A minimum of 100 plants were surveyed within any one compartment once it had been established that this provided a representative estimate of utilization (also see Schmutz 1983). Up to 400 seedlings were monitored in some large compartments however, where severe damage had been caused. Straight-line transects were used in these surveys to facilitate re-examination several months later, and the site of every fifth plant was marked with a numbered aluminium tag attached to a wooden stake. Conspicuously painted poles marked the start and end of each transect, which was sited at random but orientated towards the centre of the compartment whenever possible. This was

done because cursory examinations at the onset of this study indicated a possible "edge effect" with a higher incidence of browsing around the perimeter than in the centre of the compartment.

Initially, height measurements and counts of shoots were made in estimating utilization. Browsed portions of each plant were also marked with nail varnish to ensure that utilization estimates would not be duplicated. As I gained in experience, ocular estimates replaced those obtained from measurements. While ocular estimates are generally subjective and have an uncertain degree of accuracy (Schmutz 1983), results obtained from this means and from estimates based on measurements recorded by an independent observer showed close agreement, while ocular estimates could be conducted more rapidly and resulted in greater sample sizes. Whether estimates were made ocularly or from measurements, extensive use was made of Walker's (1976) seven damage/utilization classes, since these proved to be more comprehensive, easier to apply and more repeatable than other class intervals. Once the level of browsing had been assessed for each plant within a transect, the overall current species use was calculated using a modified version of Schmutz's (1983) method. Median values of specific browse classes (expressed as a decimal fraction) were multiplied by the % frequency of that browse class and all of these products were added to provide the current level of browse utilization (e.g. see Table 6.5). The animal group responsible for the browsing injuries was identified using Holloway's (1968) criteria.

6.2.3 Food Preferences of Bushbuck and Duiker Feeding on Commercial Timber Species

In most parts of Weza State Forest, any feeding antelope is likely tc encounter only one or two commercial timber species in its immediate surroundings. Consequently, pines might be utilized simply because alternative foods are not

available. Two plots were therefore established to determine whether bushbuck and/or duiker showed any preferences for timber species when offered a choice. The two plots were established in temporary unplanted grassland, and a grid of 10 by 10 sites were prepared using the 2,7 m spacing currently employed by the Forestry personnel for pines. Eleven individuals of nine different timber species were obtained from the Forestry nursery or from naturally regenerated seedlings within the plantation. These 99 seedlings were then planted in the prepared sites during January 1981 (an additional Pinus taeda was planted in the 100th site at one plot and an extra Pinus elliottii in the second plot). To prevent biases from possible edge effects, sites were chronologically numbered (starting at the most south-westerly corner) while the site position for each individual plant was drawn randomly. All plantings occurred during wet weather, and each plant was subsequently marked with a numbered aluminium tag attached loosely to the stem with plastic-coated wire. One individual of each species (again chosen randomly) was protected by a wire mesh enclosure supported by wooden poles. These were designed to act as controls and to facilitate utilization estimates for the unprotected specimens. Several of these enclosures were dislodged by horses however, and later many of the wire sleeves were stolen. These former controls were therefore abandoned and ignored in all subsequent assessments. Plants that died as a result of transplanting or from damage caused by rodents were replaced during the first three months with similar sized individuals, but adjustments were made to availability and utilization estimates when trees died after April 1981.

Trees were monitored every month from February 1981 to March 1982 inclusive, except in September and December 1981 and February 1982. Presence of absence of browsing was only noted in February 1981, but thereafter utilization estimates were recorded for each plant. However, deciduous plants were not monitored during periods of dormancy. As with utilization surveys, plant use was initially estimated by measurements of height, shoot lengths and the proportions of

intact and consumed shoots. Browsed portions were marked with nail varnish, and photographs of individual trees were periodically taken. Later, as a result of the experience gained from other utilization surveys, and because the trees were examined almost every month, I became familiar with the growth form of each plant, and measurements were replaced by ocular estimates, which again showed close agreement with those recorded by an independent observer. Utilization assessments were based on the use of available browse; consequently a plant that was heavily utilized in March and consumed further in April might have a lower estimate of utilization in April than the preceding month because less of the plant would be available to any browsing antelope at this time. Current species use was calculated in an identical manner to that used in transect surveys.

6.2.4 Supplementary Foods

Five small plots, each less than 1 ha in area, were ploughed and planted with seeds of fodder crops during the summer of 1981/1982. Each site was given a top dressing of commercial fertilizer (2:3:4) at an approximate rate of 100 Kg per ha, and sown with oat (Avena fatua) and Japanese radish (Raphanus sativas) seeds. All of the plots were located along an established census route and animal activities at these sites were regularly monitored each month. (The plots were also designed to examine their feasibility in attracting bushbuck and duiker for census and capture purposes.) Although this supplementary food was intended for winter use, both bushbuck and duiker were utilizing these areas heavily in March and April, and all available fodder at each plot had been consumed by the end of May. In addition to providing supplementary food, these plots showed considerable potential as sites of attraction, (particularly if they could be fenced until such times when captured animals or counts were required). However, establishing such feeding sites required an enormous amount of effort and time (apart from Forestry's assistance with

ploughing, all other work including fertilizing, seeding and watering, all done by hand, was conducted by the author and his assistant) and although additional assistance was requested from the Directorate of Forestry, this appeal was rejected and plans for further supplementary food plots had to be abandoned.

6.3 RESULTS

6.3.1 Rumen Analysis

6.3.1.1 Sieve mesh size

The entire rumen contents from five duiker were individually washed through two stacked sieves with mesh sizes of 6,35 mm and 3,18 mm. An average of 47,3 ml (± 7,1 ml S.E.) was retained on the 6,35 mm sieve and 15,8 ml (± 4,5 ml S.E.) remained on the 3,18 mm sieve. The larger sieve therefore retained approximately 75% (range 62% - 92%) of the washed rumen contents. The entire rumen contents of two other duiker were washed over the larger sieve only, and 110,1 ml and 329,5 ml of plant material were retained. Minimum and maximum values of total rumen contents trapped on the 6,35 mm sieve were obtained from animals shot during the same month (April) when less than 30 minutes separated their times of death. Because these rumen content volumes varied to such an extent, irrespective of season or time of collection, the aggregate volume method was considered to be superior to the aggregate percent method; the latter would tend to suppress the significance of full rumens and magnify the importance of foods in rumens that were relatively empty (Martin et al. 1946). Consequently, the aggregate volume method was used throughout this study.

Potential biases in dietary assessment resulting from the use of different sieve mesh sizes were examined by comparing the percentage volumes of foods trapped on the 6,35

mm and 3,18 mm sieves. There were no significant differences in plant part or species composition determined from each sieve for any of the five duiker rumens examined. However, separation and volumetric measurements took nearly half the time for fragments retained by the larger sieve (approximately 2,0 hours), compared to those obtained from the 3,18 mm sieve (3,75 hours). These records do not include the times required to wash adequately the rumen contents, which were appreciably longer for the smaller fragments.

The entire rumen contents from two bushbuck were similarly prepared and analysed. The larger mesh retained approximately 56% of the total plant material (average of 225,6 ml) trapped on both sieves. As with duiker, there were no significant differences between percent volumes of plant parts or species obtained from the two sieves for either rumen. Excluding washing, separation and volumetric measurements averaged 2,75 hours for material from the larger sieve and 6,25 hours for the smaller plant fragments. Since, in both species, the plant fragments from the larger sieve were always examined first, the time expended to identify a new species was always charged to this sample; differences in these times spent analysing different sieve contents should therefore be regarded as minimal.

Since the dietary composition of both duiker and bushbuck was unaffected by sieve mesh size, but took appreciably longer to assess when the smaller plant fragments were included, the smaller sieve was discarded and all the following results are based on material retained by the 6,35 mm mesh.

6.3.1.2 Volumes of rumen contents examined and identified

In order to test the assumption that samples removed from the rumen were representative of the total volume, the entire rumen contents from two duiker and two bushbuck were individually treated in the following manner. The contents were thoroughly mixed by hand and then emptied into a

circular bowl, where the material was divided into four approximately equal portions. The first and third quarters were combined and washed over a 6,35 mm sieve. Plant parts and species composition were then compared to those from the second and fourth quarters which had been treated in an identical manner. Dietary composition differences between the two halves of the rumen were insignificant for all four animals examined. Consequently, rumen contents were always thoroughly mixed before sub-samples were removed whenever rumen content volumes were too great to examined in their entirety.

A total of 5 887,65 ml of sieved rumen contents were examined from 124 duiker (average volume 47,5 ml per animal), of which 5 631,55 ml (95,7%) were identified to species of genus level. Rumen content volumes examined from 159 bushbuck totalled 5 112,85 ml (average volume 32,2 ml per animal) but only 2 000,9 ml (39,1%) were identified. Several factors may have been responsible for this lower proportion of identified bushbuck food. Firstly, in keeping with the emphasis of this study, reference plant collections were largely confined to plantations (where 74% of all duiker but only 56% of all bushbuck were culled, see Fig. 6.1), grasslands and cultivated areas, while the relatively few indigenous plants collected were from riverine and forest margin areas. Consequently, while much of the material from bushbuck rumens may have been discernible, it could not be positively identified. Secondly, the lower proportion of bushbuck rumen material retained on the 6,35 mm sieve (see 6.3.1.1.) demonstrate that plant fragments from this species were generally smaller than those from duiker (also see Plate 3). Because of their larger mouth and body size, it is unlikely that bushbuck selected smaller plant parts than duiker (see Jarman 1974; Hanley 1982), while differences in the activities of these two species immediately before individuals were shot (Fig. 6.2) suggest that rumination was not responsible for the smaller plant parts collected from bushbuck. A more plausible explanation is that bushbuck masticate their food more than duiker before ingestion (see Plate 3), but, whatever the cause, the smaller items made

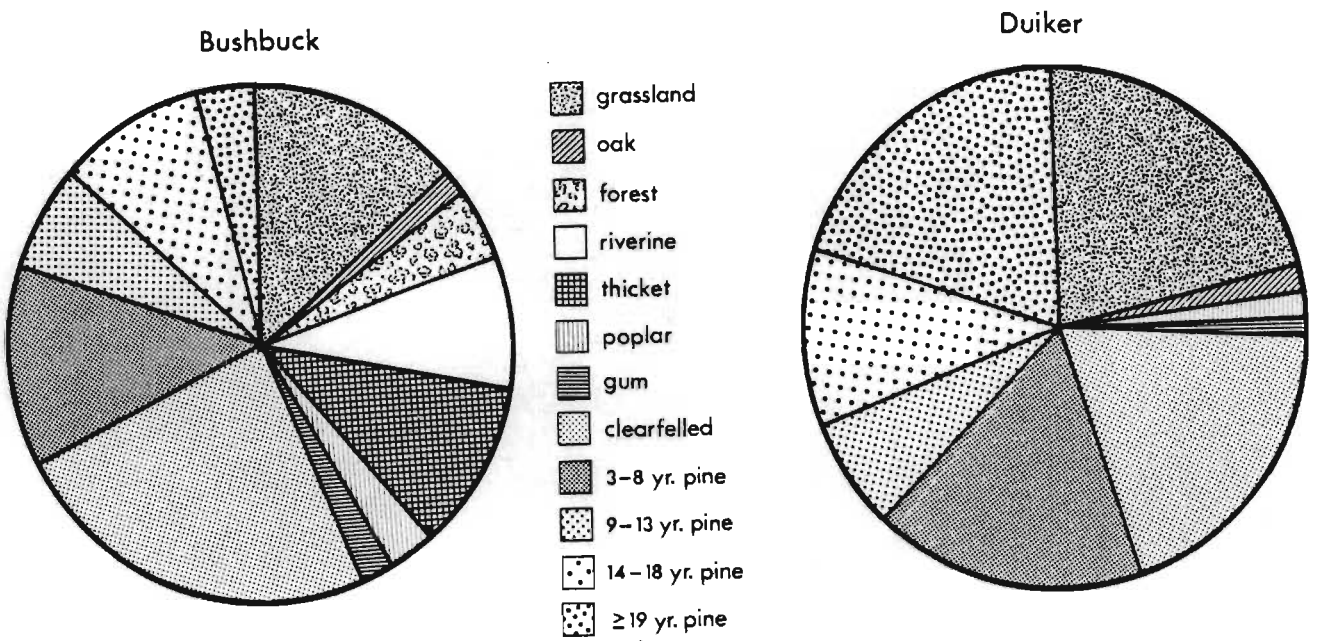


FIGURE 6.1 The proportions of bushbuck (n=129) and duiker (n=116) culled in the major habitats of Weza State Forest.

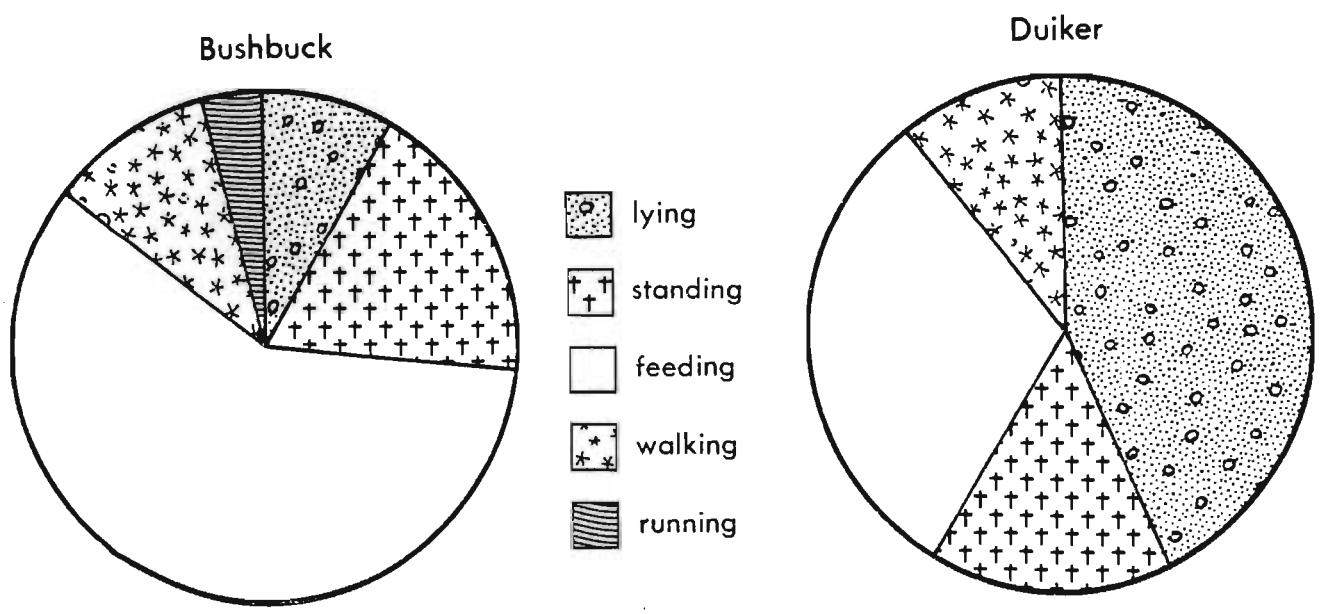


FIGURE 6.2 Activities of bushbuck (n=129) and duiker (n=116) immediately prior to their collection for diet assessment purposes.

Plate 3

identification of bushbuck diets much more difficult.

An estimate of sample size adequacy was computed using the statistical methods recommended by Hanson and Graybill (1956). Both sample sizes of 124 duiker and 159 bushbuck rumens provided an adequate estimate of major food items within 10% of the true mean at the 95% confidence level. It is within this context that the following results are presented and discussed.

The identified proportions of plants eaten by duiker each month remained relatively constant throughout the year (Fig. 6.3). In contrast, the proportions of bushbuck rumens

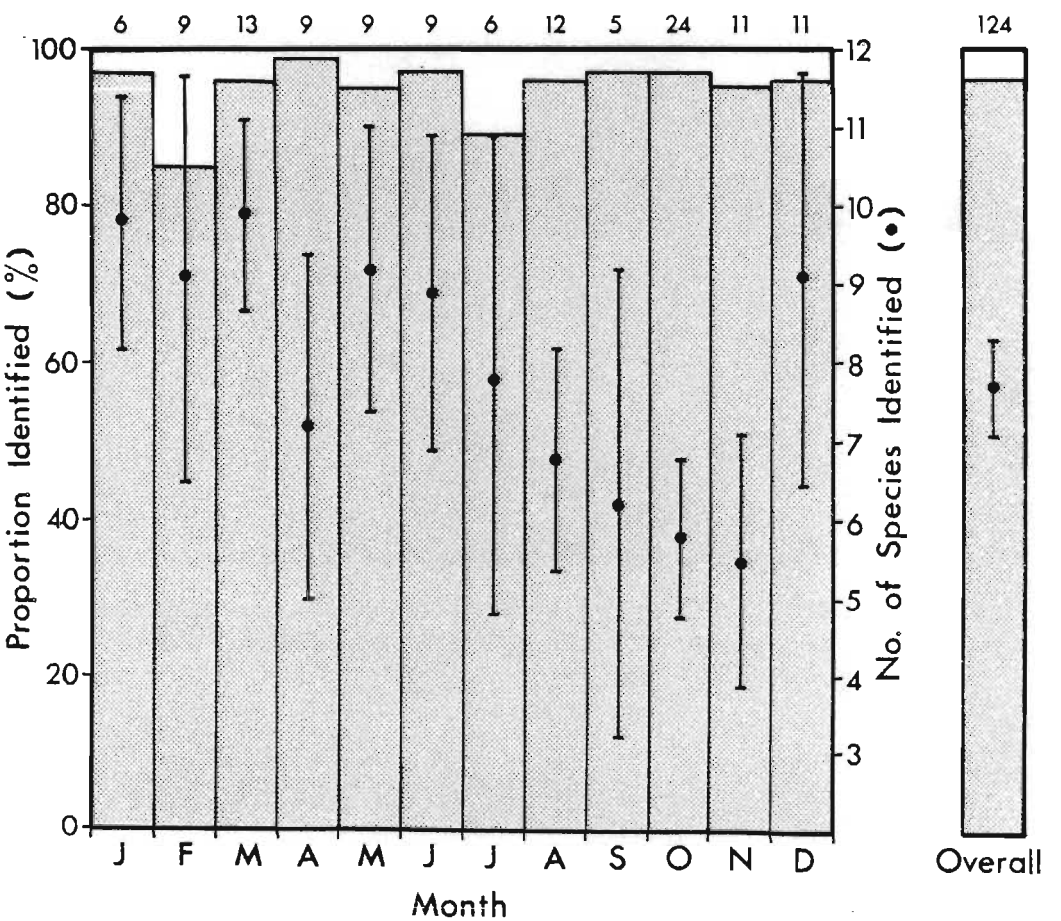


FIGURE 6.3 Monthly variation in the relative proportions of identified rumen contents (aggregate volume) and numbers of identified plant species consumed by duiker. (Mean values are shown ± two standard errors; values at the top of the figure relate to monthly samples of rumens examined).

that could be identified were greatest in winter and early spring, and minimal during the summer months (Fig. 6.4). However, in terms of the number of plant species identified, both antelopes ate significantly fewer plant species in spring than in winter ($t=3,02$; $p<0,01$, and $t=4,04$; $p<0,001$ for duiker and bushbuck respectively) or during summer ($t=4,80$; $p<0,001$, and $t=2,08$; $p<0,05$ respectively). All other seasonal differences in the number of species identified were not significant with the exception that bushbuck consumed fewer plant species in summer compared to autumn ($t=2,33$; $p<0,05$). Monthly variations in the numbers of species identified in duiker and bushbuck rumens are illustrated in Fig. 6.3 and Fig. 6.4 respectively.

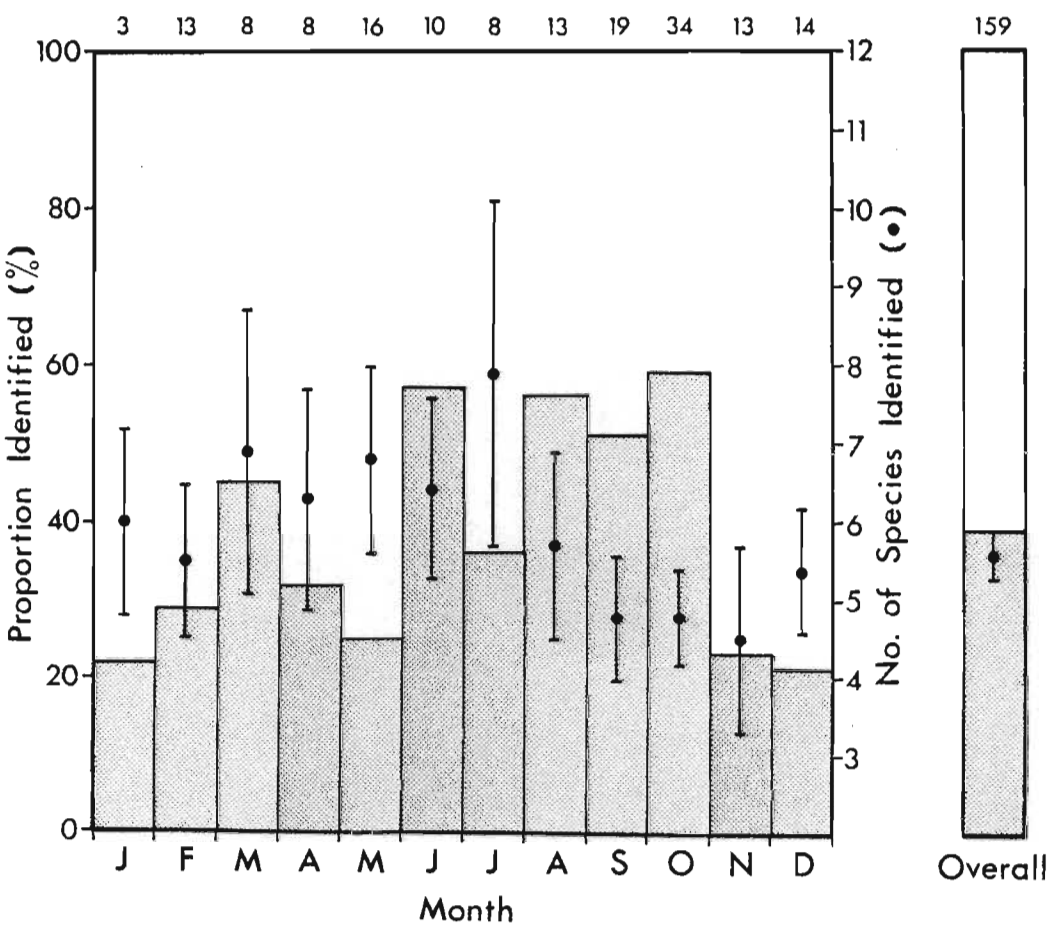


FIGURE 6.4 Monthly variation in the relative proportions of identified rumen contents (aggregate volume) and numbers of identified plant species consumed by bushbuck. (Mean values are shown ± two standard errors; values at the top of the figure relate to monthly samples of rumens examined).

6.3.1.3 Plant parts consumed

a) Duiker

On an annual basis, fruits and seeds (mast) constituted the largest portion (37,9% by volume) of the diet eaten by duiker. Other plant parts of major importance to this species included fungi (28,2%) and dicotyledonous leaves (26,6%) while stems (3,0%) leaves and stems (3,0%), flowers (1,0%) and grass (0,3%) made up the remainder of the diet. Browse (leaves and/or stems from dicotyledonous plants) therefore accounted for 32,6% of the total dietary volume.

Duiker consumed greater quantities of fruits and seeds during winter (49,9%) than at any other time of the year, although seasonally these always accounted for at least 25% of the diet and were least utilized during the spring. Fungi were most important during autumn and winter (36,8% and 31,5% respectively), and accounted for 12% of the diet during the remaining seasons. Browse formed the majority of the plant parts eaten during spring (58,3%) and summer (58,0%) but contributed only 18,5% of the winter diet, when more stems (4,5%) were eaten than at any other time of the year. Both flowers and grass, although food items of minor importance, were consumed in greatest quantities during spring (3,1% and 0,9% respectively) and least during winter when both were recorded as trace values. Monthly variations in the proportions of plant parts eaten by duiker are illustrated in Fig. 6.5. Seasonal and overall differences in the proportions of plant parts eaten by males and females were not significant and consequently the diets from both sexes were combined in all subsequent analyses.

b) Bushbuck

In contrast to the quantity taken by duiker, browse formed 89,5% of the food eaten by bushbuck, and largely consisted of leaves (53,1%) and stems (28,3%). Bushbuck ate

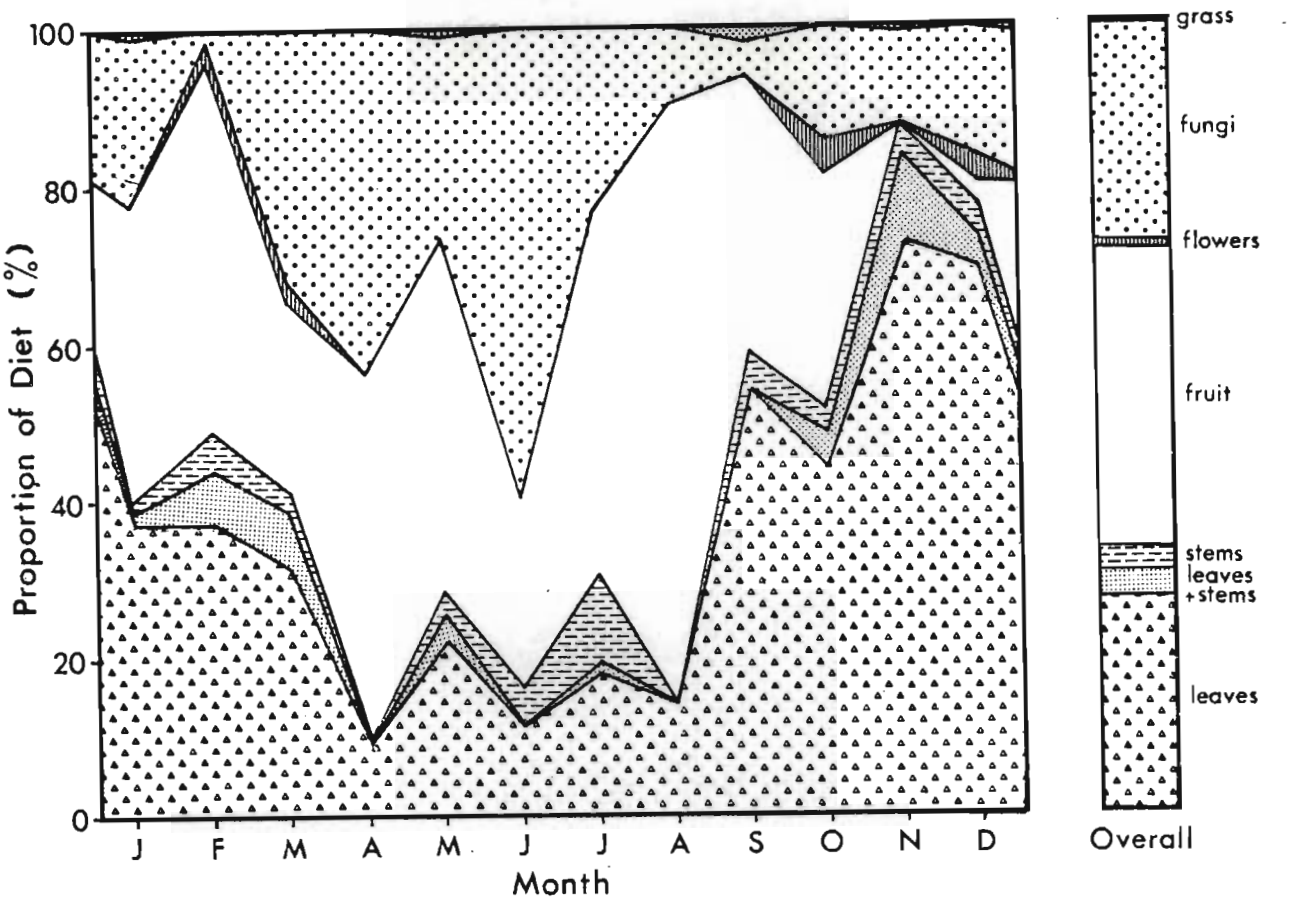


FIGURE 6.5 Monthly variation in the proportions (aggregate volume) of plant parts eaten by duiker in Weza State Forest.

smaller quantities of fruits and seeds (5,9%) and grass (2,9%) while fungi and dicotyledonous flowers were of minimal importance (0,9% and 0,8% respectively).

The proportions of browse consumed by bushbuck were lowest in winter (78,7%) and spring (87,1%) and resulted from a decline in the quantities of both leaves and stems eaten during these months. Grass was of greater importance at these times (3,8% and 7,6% respectively) than during summer or autumn when it formed less than 1% of the diet. Browse and grass together accounted for over 90% of all foods consumed in all but two months of the year (June and July) when the remainder of the diet consisted largely of fruits and seeds (Fig. 6.6). With the exception of trace amounts, fungi were found in bushbuck rumens only during winter (0,9%) and in spring (2,8%). Significant seasonal differences in plant part usage between the sexes were not evident and

therefore all subsequently analyses included material from both male and female bushbuck.

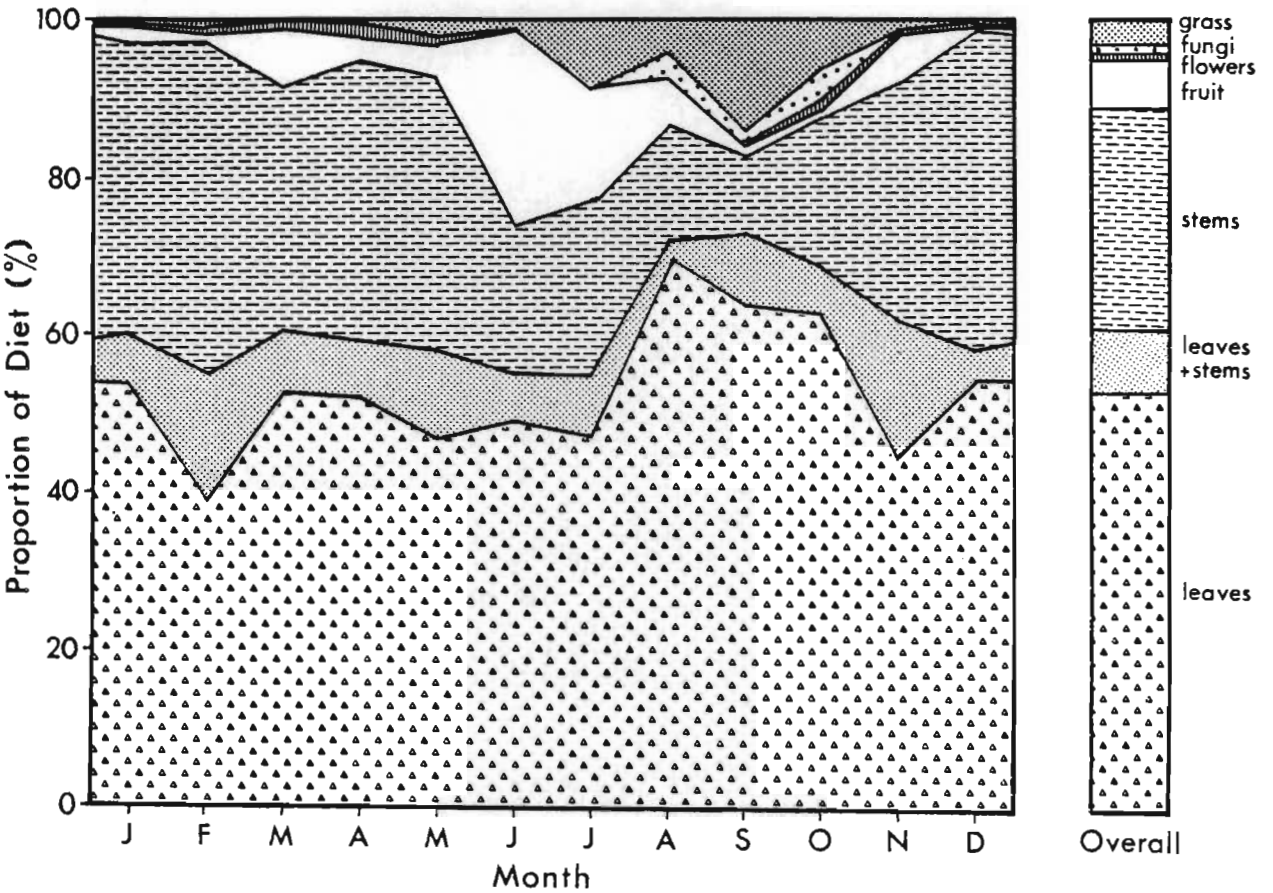


FIGURE 6.6 Monthly variation in the proportions (aggregate volume) of plant parts eaten by bushbuck in Weza State Forest.

c) Forage overlap

Based on the plant parts common to both ungulates' diets, forage overlap during the year was 40,5% but ranged from 30,3% during autumn (13,4% in April) and 64,5% during the spring months.

6.3.1.4 Forage classes consumed

a) Duiker

The majority of the identified food items eaten by duiker were from shrubs and trees (54,5%), fungi (see above)

and forbs (14,4%). Shrubs and trees were utilized most during spring (77,9%) and least during autumn (45,9%). Forbs accounted for only 7,7% and 6,8% of the diet during winter and spring respectively but increased to 28,2% in the summer months before declining in autumn (14,7%). Ferns were utilized at low levels throughout the year (Fig. 6.7).

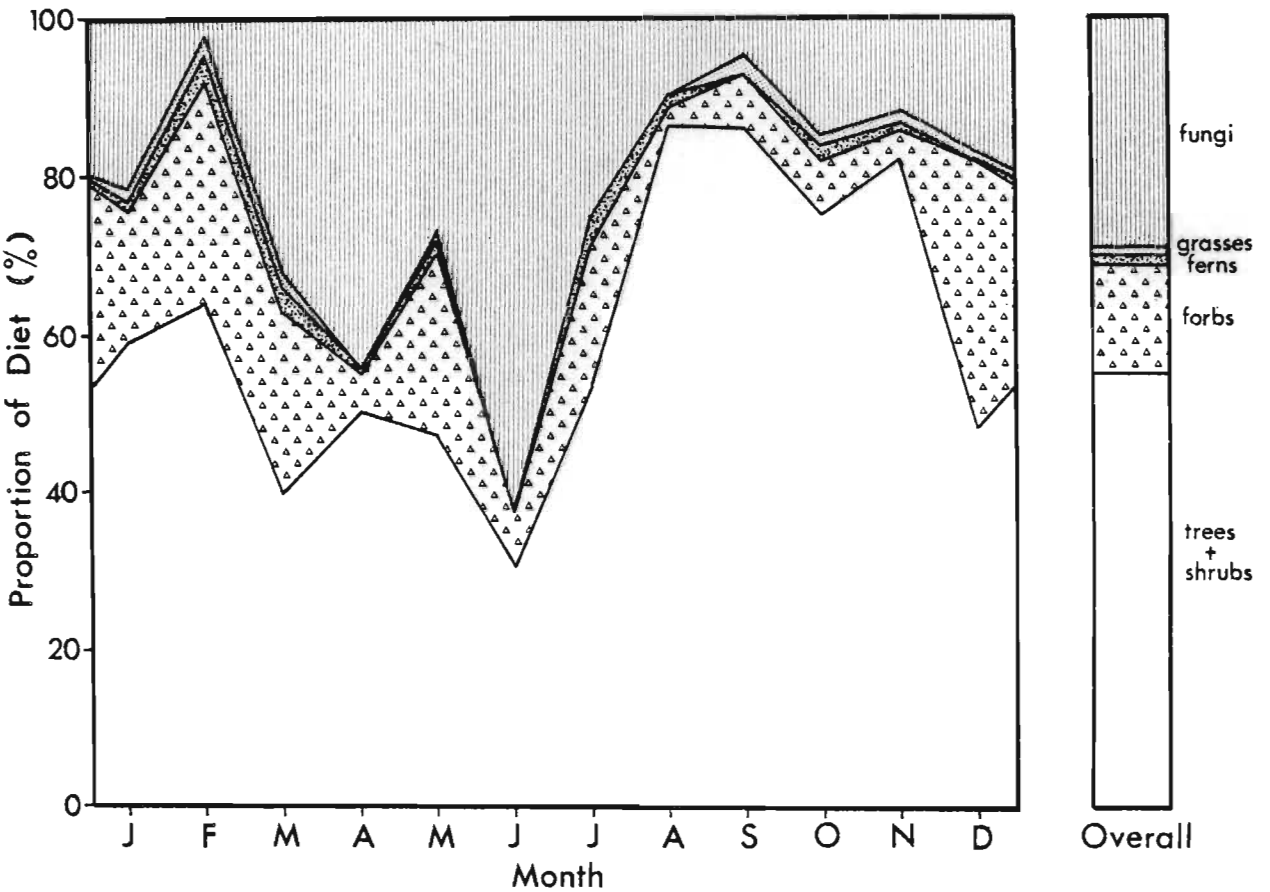


FIGURE 6.7 Monthly variation in the forage class composition (aggregate volume) of the diet of duiker in Weza State Forest. (The relative contributions of each forage class were determined from the identified portions of rumen contents).

b) Bushbuck

Food items from shrubs and trees dominated the annual identified diet of bushbuck (60,6%), were eaten in greatest quantities during spring (67,8%), and never declined below 50% during any season. Forbs ranked second (19,9%) and, in

contrast to the duiker, bushbuck consumed the greatest proportions of forbs in winter (34,1%), but had similar minimal quantities during spring (5,7%) when early growth from deciduous shrubs and trees provided alternative foods. Ferns (overall volume of 9,6%) were heavily utilized during the summer months (Fig. 6.8) when they comprised 31,0% of the identified diet and were least important during the winter. Grass and fungi consumption increased during this time and peaked during the spring (see above and Fig. 6.8). Bryophytes were only found in measurable amounts during February (Fig. 6.8).

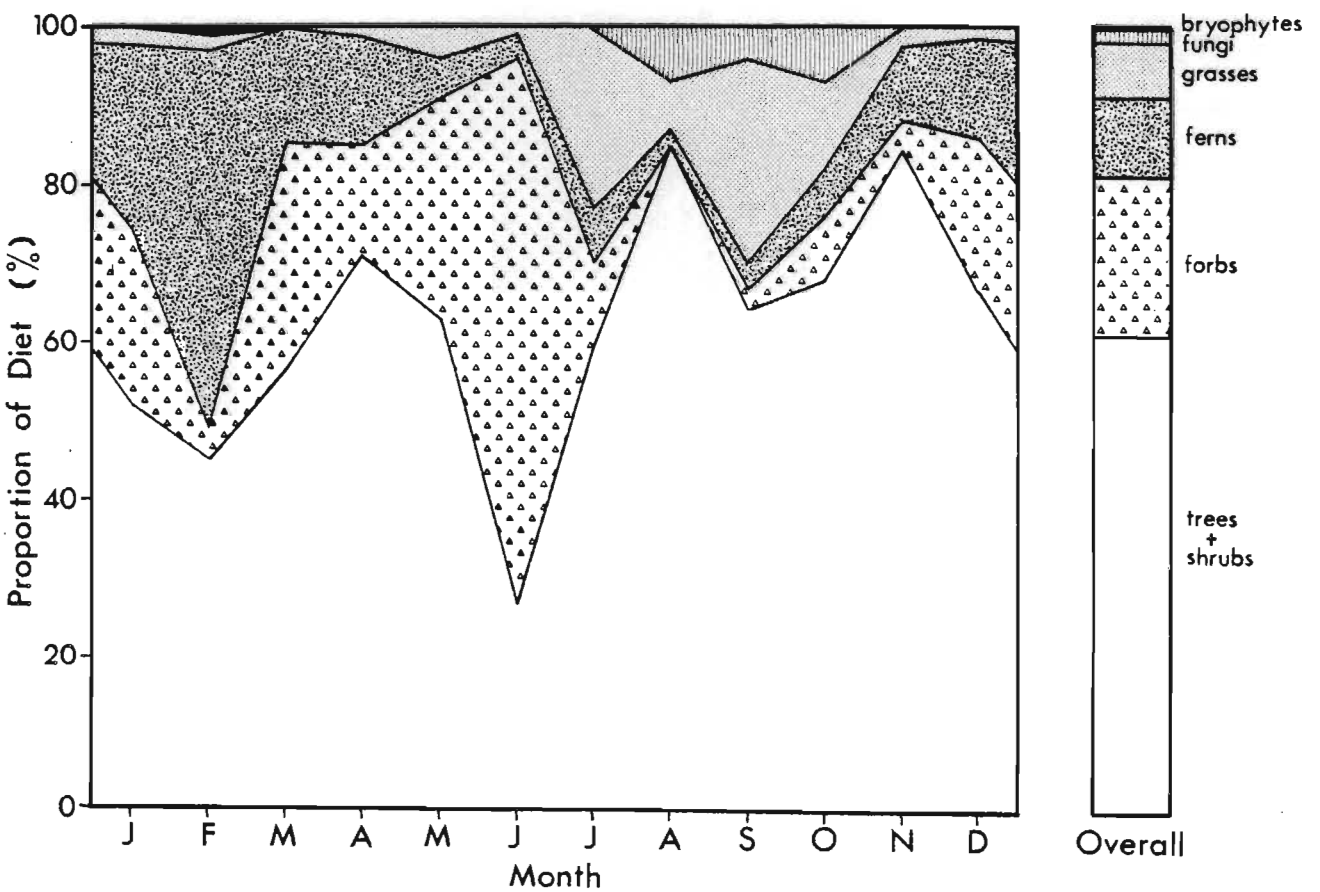


FIGURE 6.8 Monthly variation in the forage class composition (aggregate volume) of the diet of bushbuck in Weza State Forest. (The relative contributions of each forage class were determined from the identified portions of rumen contents).

c) Forage overlap

During the year the estimated overlap in forage class selection (identified species only) was 55,2%. Forage class overlap was greatest during spring (62,5%) and declined throughout summer, autumn and winter (61,7%, 47,1% and 40,9% respectively).

6.3.1.5 Plant species consumed

a) Duiker

A total of 61 food items eaten by duiker were identified, usually to species or genus level. Of these, only eight (Rubus cunifolia, Solanum mauritianum, Acacia mearnsii/A.dealbata, Acacia melanoxylon, Pellaea viridis, fungi, grasses and brown Pinus spp. needles) were consumed in varying quantities during every month of the year, while a total of 22 species (36%) were eaten for half the year or less, and 19 (31%) species were taken during any single month. The greatest variety of foods, 31 identified, plants were consumed during February and the least variety, consisting of 15 species, occurred in September. Seasonally, diet diversity remained relatively constant throughout much of the year (the maximum number of species eaten was 41 in autumn) but declined notably during spring when duiker fed on only 31 identified plants.

The ten most frequently eaten plants, listed in decreasing order of percentage occurrence, were:

Rubus cunifolia	82%
Fungi	71%
Acacia spp. (Wattles)	65%
Pellaea viridis	61%
Grasses	60%
Acacia melanoxylon	48%
Pinus spp. (brown needles)	46%
Pinus spp. (green needles)	40%

Solanum mauritianum	40%
Galopina circaeoides	24%

Overall, 15 items exceeded 1,0% by volume and accounted for more than 85% of the total volume of forage eaten. These and all other identified foods are listed by volumetric composition in Appendix C.2 which also includes monthly frequency of occurrence data (decimal values). Monthly variations in the proportions (% volume) of the major plant species or groups eaten by duiker are illustrated in Fig. 6.9.

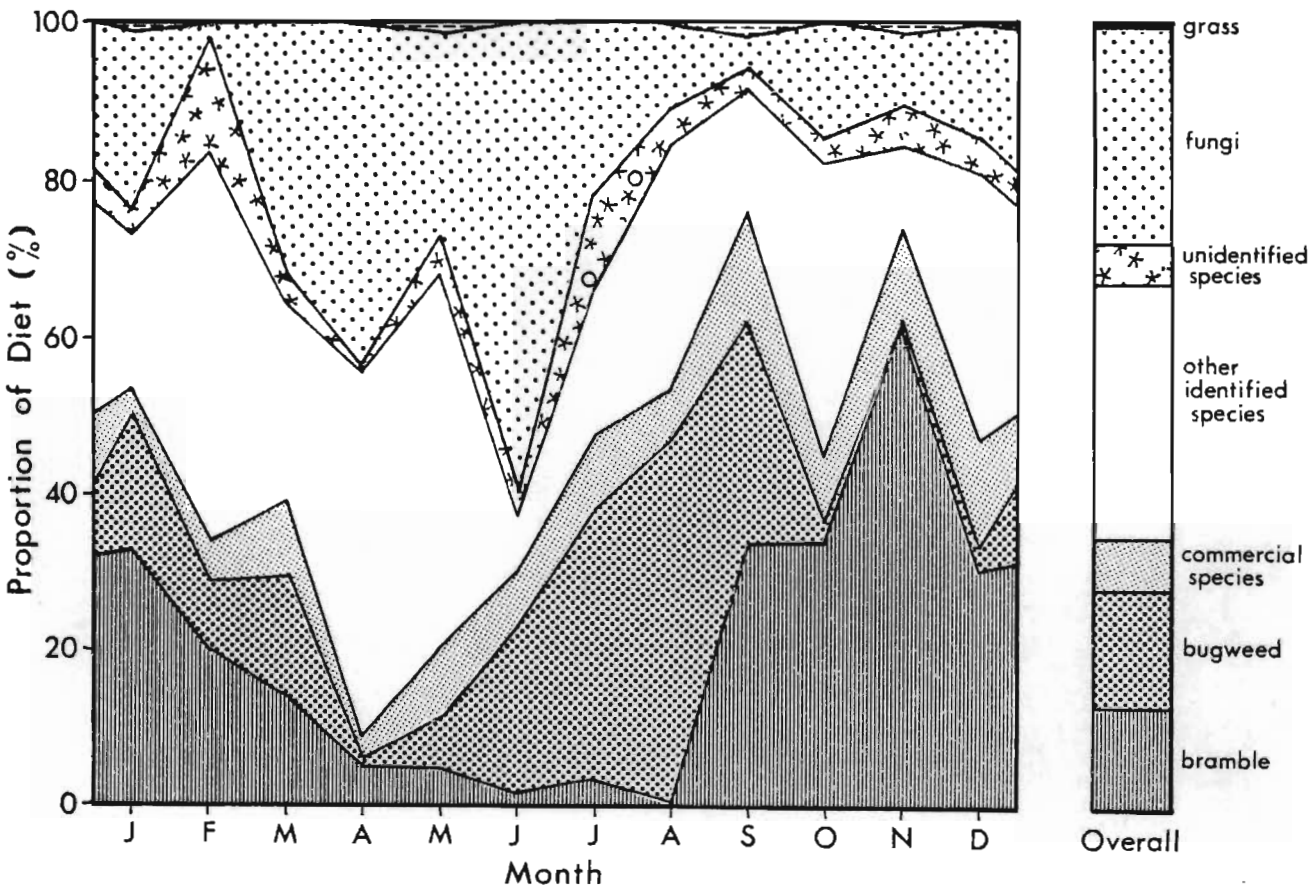


FIGURE 6.9 Monthly changes in the principal components (aggregate volume) of the diet of duiker in Weza State Forest.

All plants with a monthly PFI value equal to or greater than 0,05 are listed in Table 6.1 on the basis of their overall percentage contribution to the diet. Fungi were

almost twice as important than any other food item, and accounted for at least 20% of the diet for eight months of the year and for over 40% during autumn and early winter. The next most important food was Rubus cunifolia, particularly during spring (almost entirely buds and leaves) and summer (when fruits became available and comprised up to 56% of the total volume of bramble eaten). This species was of negligible importance during the winter months, undoubtedly because the plants offered little green browse at this time, but duiker consumed large quantities of the third most important food, Solanum mauritianum fruits, during this period, and in early spring. Other leading plant species included Acacia melanoxylon and other Acacia species (mainly A. mearnsii and A. dealbata) as well as Pellaea viridis although all of these never exceeded a % PFI value of 10% during any month of the year. Acorns were consumed during late autumn and to a lesser extent during winter, while the greatest quantities of green Pinus needles were taken during winter and spring, but particularly during September (Table 6.1). Other foods of less importance but which contributed a minimum of 3% to the diet during any one month include the forbs Acalypha punctata and Acalypha schinzii (both in December), Physalis peruviana (July), brown Pinus needles (June), Solanum aculeastrum (February), Solanum nigrum (April), Crataegus pubescens (April and September), Galopina circaeoides (May) and Ficus carica (February). Many of the other foods taken by duiker were from exotic trees, shrubs and crops growing in old homestead or cultivated areas (Table 6.1).

b) Bushbuck

Bushbuck consumed a total of 47 identified food items, although the high proportion of unidentified rumen contents suggest that many more plans are eaten by this species. Six of these foods were eaten throughout the year, and all were also consumed every month by duiker (Rubus cunifolia, Acacia melanoxylon, other Acacia spp., Pellaea viridis, brown Pinus spp. needles and grasses). Only 11 species (23%) were eaten for half the year or less, while the consumption of 15 other

TABLE 6.1 Major foods of duiker at Weza State Forest between September 1980 and July 1984 as determined by rumen content analysis. (Values are expressed as percentage composition of annual or monthly principal food indices; see text for details).

Species	Over-all	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Fungi	42,4	31,7	1,6	47,2	69,1	46,4	70,7	21,5	7,5	4,2	20,0	4,8	20,0
Rubus cunifolia	22,6	46,6	37,6	17,9	6,2	9,1	1,4	3,2	0,1	42,7	62,3	77,0	40,6
Solanum mauritianum	12,7	8,2	7,4	12,7	0,5	5,2	15,8	40,7	70,8	25,7	1,1	tr.*	0,5
Unidentified	8,7	4,2	29,0	4,9	1,0	9,6	3,4	16,5	6,2	5,3	5,6	6,2	5,5
Acacia mearnsii/A.dealbata	3,6	1,0	6,8	4,5	0,2	3,6	0,5	3,8	5,0	0,3	0,8	8,4	5,7
Acacia melanoxylon	1,8	1,3	0,6	1,1	0,2	5,7	3,6	0,2	0,7	0,4	0,6	tr.	3,9
Pellaea viridis	1,3	0,5	3,8	2,6	0,4	0,7	0,1	1,3	0,1	0,2	2,5	0,8	tr.
Quercus robur	1,1				9,3	11,0		0,2	4,3				
Pinus spp. (brown)	1,0	tr.	tr.	0,2	0,5	0,2	0,2	5,2	1,6	14,1	1,7		tr.
Acalypha punctata	0,7	2,8	tr.	0,1	0,2				0,1		0,4	0,5	10,0
Acalypha schinzii	0,6	0,7		1,7	tr.						tr.	0,6	10,8
Pinus spp. (green)	0,5	0,1	tr.	0,9	tr.	0,1	3,0	tr.	tr.	tr.	tr.	tr.	0,5
Solanum aculeastrum	0,5		4,0	1,3	0,9	tr.	0,5	0,3	tr.		tr.		
Grasses	0,4	0,8	0,1	0,3	tr.	1,0	tr.	tr.	0,1	2,0	0,6	0,7	0,2
Crataegus pubescens	0,3				3,3					3,9	2,1		
Solanum nigrum	0,3	0,3	tr.	0,3	7,6	0,2							tr.
Galopina circaeoides	0,3	1,1	0,1	tr.	0,1	3,6	tr.	0,8	tr.		tr.	0,3	0,4
Physalis peruviana	0,3	tr.	tr.	0,4		2,0	tr.	5,9	tr.				
Pentanisia prunelloides	0,3	0,2	0,3	1,7	0,1		tr.			0,1			1,5
Taraxacum officinale	0,3	0,1	1,0		tr.	0,9	tr.	0,2			1,5	0,2	0,3
Acalypha ecklonii	0,1		0,5	2,1		tr.				0,4			
Prunus persica	0,1		1,0			0,1			0,3		tr.	tr.	
Halleria lucida	tr.	tr.	0,7			0,2	tr.	tr.	tr.		tr.	tr.	
Cupressus lusitanica	tr.	tr.		tr.	tr.				tr.		0,8		tr.
Ficus carica	tr.		3,0										
Solanum tuberosum	tr.		1,8										
Duchesnia indica	tr.		0,6		tr.	tr.		0,1	0,1		tr.		
Zea mays	tr.		0,4										
Populus deltoides	tr.					0,2					0,2	tr.	
Phytolacca heptandra	tr.			0,1	tr.		0,6	tr.					
Podocarpus henkelii	tr.								0,9				
Citrus aurantium	tr.								1,1				
Ligustrum sp.	tr.	tr.	tr.			tr.	tr.		0,4		tr.	0,1	tr.
Cotoneaster pannosa	tr.	tr.							0,2				
Morus alba	tr.								0,1				
Carpobrotus dimidiatus	tr.		tr.						0,1				
Citrus limon	tr.								0,1				
Leucosidea sericea	tr.									0,9	0,1		
Melia azedarach	tr.										0,2		
Calpurnia aurea	tr.	tr.		tr.	tr.		tr.		tr.		tr.	0,5	tr.

*tr. - indicates trace, i.e. (0,1%

food items (32%) was confined to single months. More food items were eaten during May than in any other month, but the least variety, 9 species eaten in January is considered to be an artefact of sample size (only three bushbuck rumens examined) since the numbers of identified forage species eaten during the preceding and succeeding months were 16 and 17 respectively. Seasonally, diet diversity was greatest in autumn (32 species) and lowest in summer (22 species).

The ten most frequently eaten plants, listed in decreasing order of occurrence were:

Pellaea viridis	92%
Rubus cunifolia	74%
Grasses	72%
Pinus spp. (brown needles)	70%
Acacia melanoxylon	60%
Acacia mearnsii/A. dealbata	47%
Solanum aculeastrum	18%
Solanum mauritianum	14%
Halleria lucida	14%
Pinus spp. (green needles)	11%

With the exception of Halleria lucida and Solanum aculeastrum (which were respectively eaten by 11% and 15% of the 124 duiker examined) all of these species were also among the 10 most commonly consumed by duiker. Overall, only 10 species each contributed at least 1,0% by volume but together accounted for 32% of the total dietary volume. The monthly proportions that these and all other identified foods contributed towards the diet, together with their frequency of consumption, are presented in Appendix C.3. Exotic weeds occurring in the plantations were eaten every month but bushbuck rarely fed on Solanum mauritianum fruits (no other part of this species was eaten by either antelope) except during the winter months, even though these were available throughout the year. Buds and leaves of Rubus cunifolia became an important food during the spring and to a lesser extent in summer (Fig. 6.10), but the fruits of this species were only found in bushbuck rumens during January. Browse

from commercially important timber species was also utilized throughout the year, but particularly during autumn and late winter (Fig. 6.10).

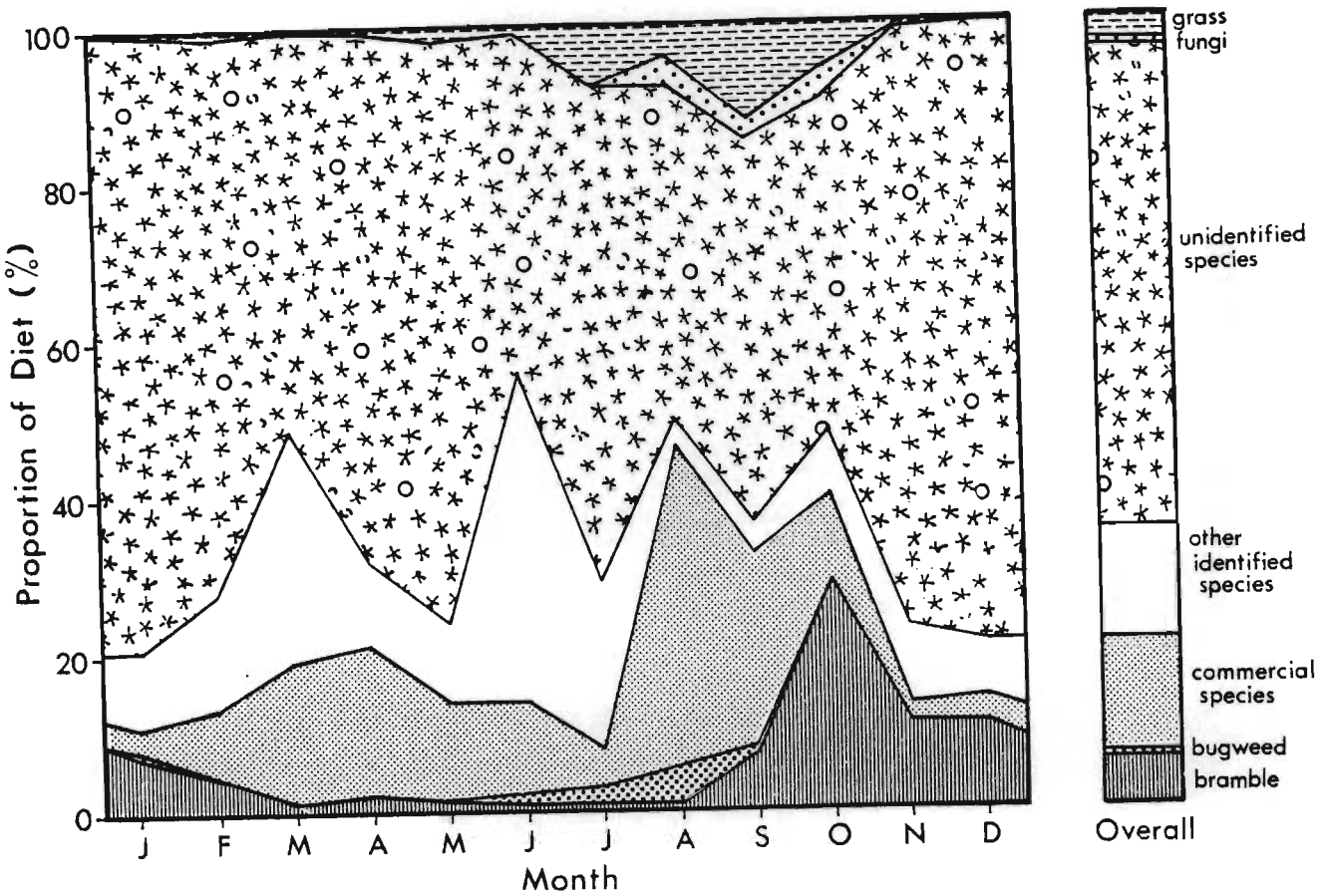


FIGURE 6.10 Monthly changes in the principal components (aggregate volume) of the diet of bushbuck in Weza State Forest.

Plant species with a PFI value equal to or greater than 0,05 during any one month are listed in Table 6.2 on the basis of their percentage importance to the diet. In contrast to duiker, none of these exceeded an overall % PFI value greater than 10%, largely because of the large quantities of unidentified forage taken by bushbuck. Major items of the diet, listed in decreasing order of importance, included Rubus cunifolia, Acacia melanoxylon, Pellaea viridis, grasses and other Acacia species, and with the exception of wattles, all of these contributed a minimum of 10% to the diet during at least one month of the year. Other less important species with minimum % PFI values of 2% in any month included Solanum aculeastrum, Solanum mauritianum,

TABLE 6.2 Major foods of bushbuck at Weza State Forest between September 1980 and July 1984 as determined by rumen content analysis. (Values are expressed as percentage composition of annual or monthly principal food indices; see text for details).

Species	Over-all	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Unidentified	78,2	82,7	77,8	69,1	72,9	84,8	59,3	76,8	58,1	71,1	51,3	87,4	84,5
Rubus cunifolia	6,1	2,9	2,9	1,1	2,0	1,2	0,6	1,0	0,4	5,6	35,2	8,6	9,0
Acacia melanoxylon	5,6	0,3	0,5	13,7	18,9	4,6	11,8	2,0	24,7	1,9	1,3	0,4	1,1
Pellaea viridis	4,4	5,6	15,2	8,5	3,9	1,3	2,3	2,6	1,4	2,1	4,3	2,1	2,8
Grasses	2,7	0,3	0,3	0,2	0,3	0,9	0,6	10,1	3,6	16,2	5,2	0,3	0,1
Acacia mearnsii/A.dealbata	1,0	0,1	1,9	0,3	0,5	4,2	1,8	1,5	0,2	0,6	0,1	tr.*	0,1
Solanum aculeastrum	0,6		0,2	0,1	0,1	1,8	18,5	0,6			tr.		tr.
Eucalyptus spp.	0,3			tr.					8,5	1,6	1,0		
Pinus spp. (brown)	0,3	0,3	0,3	0,4	tr.	0,3	0,2	0,5	0,3	0,3	0,6	0,3	0,3
Solanum mauritianum	0,2	0,4	0,1	tr.		0,1	0,5	1,9	2,2	0,2		0,1	
Halleria lucida	0,1		0,1	0,2	0,6	0,4	0,6	tr.	0,3		tr.	tr.	tr.
Fungi	0,1			0,1					0,4	0,3	0,5		
Acalypha punctata	0,1					tr.					0,1	0,1	1,8
Phytolacca heptandra	0,1					tr.	3,8			tr.			
Pinus spp. (green)	0,1		tr.		tr.	tr.		0,2	tr.	tr.	0,4	tr.	tr.
Clematis brachiata	0,1	1,6		4,1		0,1							tr.
Quercus robur	tr.			1,4		tr.		1,5					
Populus deltoides	tr.	0,6	0,7	0,6					tr.			0,1	
Pentanisia prunelloides	tr.		tr.			0,2						tr.	tr.
Bidens biternata	tr.				0,2	tr.	tr.	tr.				tr.	
Solanum nigrum	tr.				0,2	0,1							
Galopina circaeoides	tr.		0,1								tr.	tr.	
Duchesnia indica	tr.			0,2									
Physalis peruviana	tr.				tr.		0,1	0,2					
Melia azedarach	tr.				0,1								
Lilium regale	tr.				0,1								
Cotoneaster pannosa	tr.					tr.		0,5					
Cirsium vulgare	tr.							0,3					
Acalypha schinzii	tr.							0,3					
Drougetia urticaefolia	tr.									0,1			
Citrus limon	tr.											0,5	

*tr. - indicates trace, i.e. (0,1%

Eucalyptus spp., Phytolacca heptandra (all during the winter months) and Clematis brachiata (March). Dead needles from Pinus species consistently had higher % PFI values than green needles although since neither had values exceeding 1,0% at any time of the year, pine browse cannot be considered as an important component of the bushbuck diet. Bushbuck fed on a number of exotic trees, shrubs and cultivated plants, although as with duiker, these were eaten irregularly or by few individuals and consequently were of minor importance (Table 6.2).

c) Diet overlap

In terms of their % PFI values, the annual diets of bushbuck and duiker overlapped by only 11,9%, of which bramble contributed the major portion of 6,1%. Seasonally, food similarities were greatest during the spring (20,0%) and again largely resulted from the importance of bramble (minimum % PFI of 17,0%) in the diets of both these species. Diet overlap declined during summer (10,6%) and autumn (8,8%) and was lowest during winter (7,1%). The seasonal % PFI values of the major plants (with a minimum % PFI value of 4,0% for at least one season) eaten by either or both antelope species are illustrated in Fig. 6.11. On a monthly basis, bushbuck and duiker diets were most similar during October (overlap 40,0%) and least similar in March when the estimated level of diet overlap was only 3,1%.

6.3.1.6 Commercial species consumed

As a group, commercial timber species were browsed by both duiker and bushbuck throughout the year (Figs. 6.9 and 6.10 respectively). In order to determine the relative importance of each species, all records of either antelope feeding on brown pine needles have been omitted, since the consumption of these is considered to be of negligible importance in terms of potential damage or conflict with forestry management.

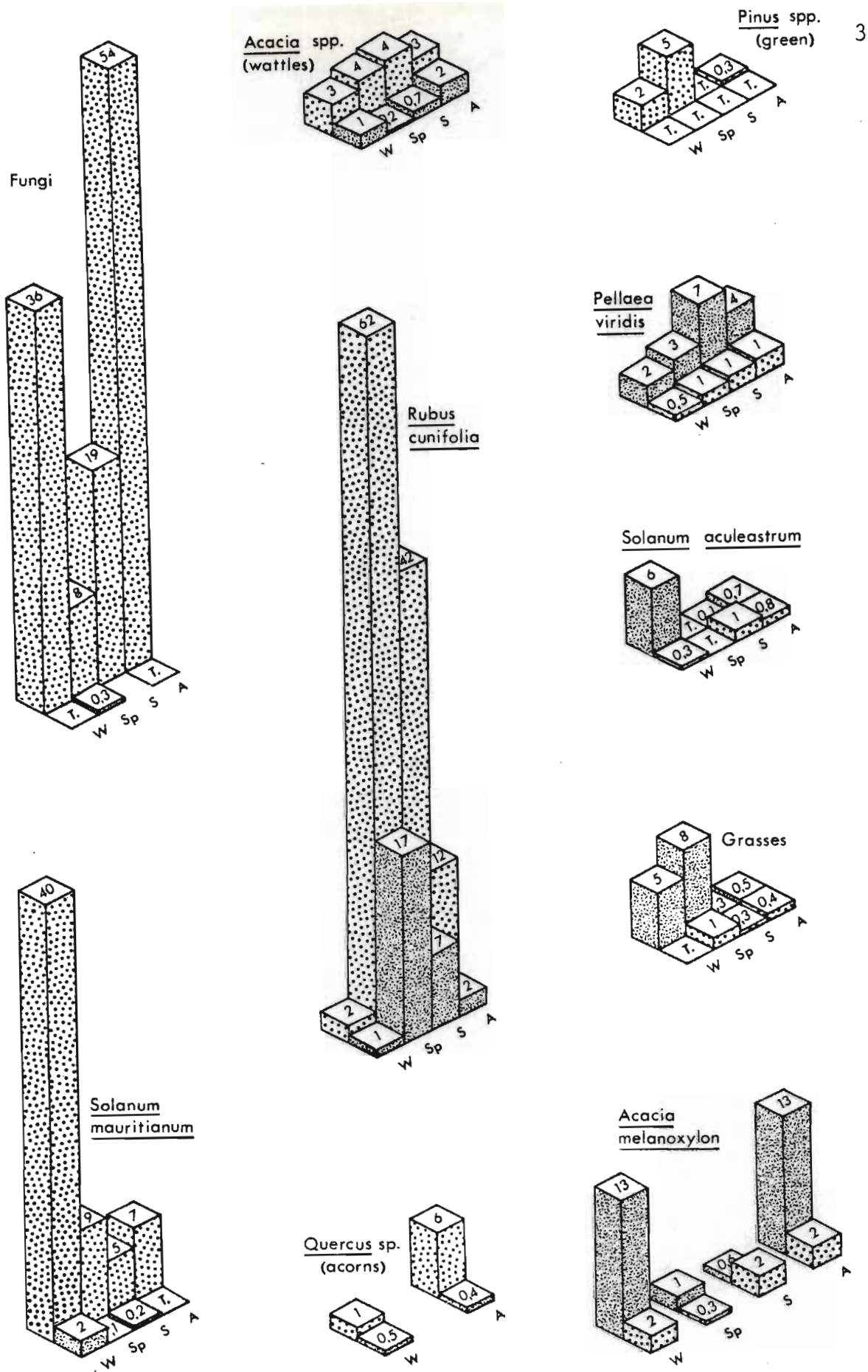


FIGURE 6.11 Seasonal variation in the importance of principal foods of duiker (stippled) and bushbuck (shaded) in Weza State Forest. (W=winter; Sp=spring; S=summer; A=autumn; %PFI values are shown to the nearest integer if these exceeded 1,0%; T=trace, i.e.<0,1%).

a) Duiker

Browse from timber species accounted for 6,1% of the annual diet of duiker, was eaten in greatest quantities (9,1% of the diet) in spring and was least important during autumn (4,9%). The monthly proportions of browse from commercial softwoods and hardwoods consumed by duiker ranged from 1,7% in April to 12,4% in September (Fig. 6.12).

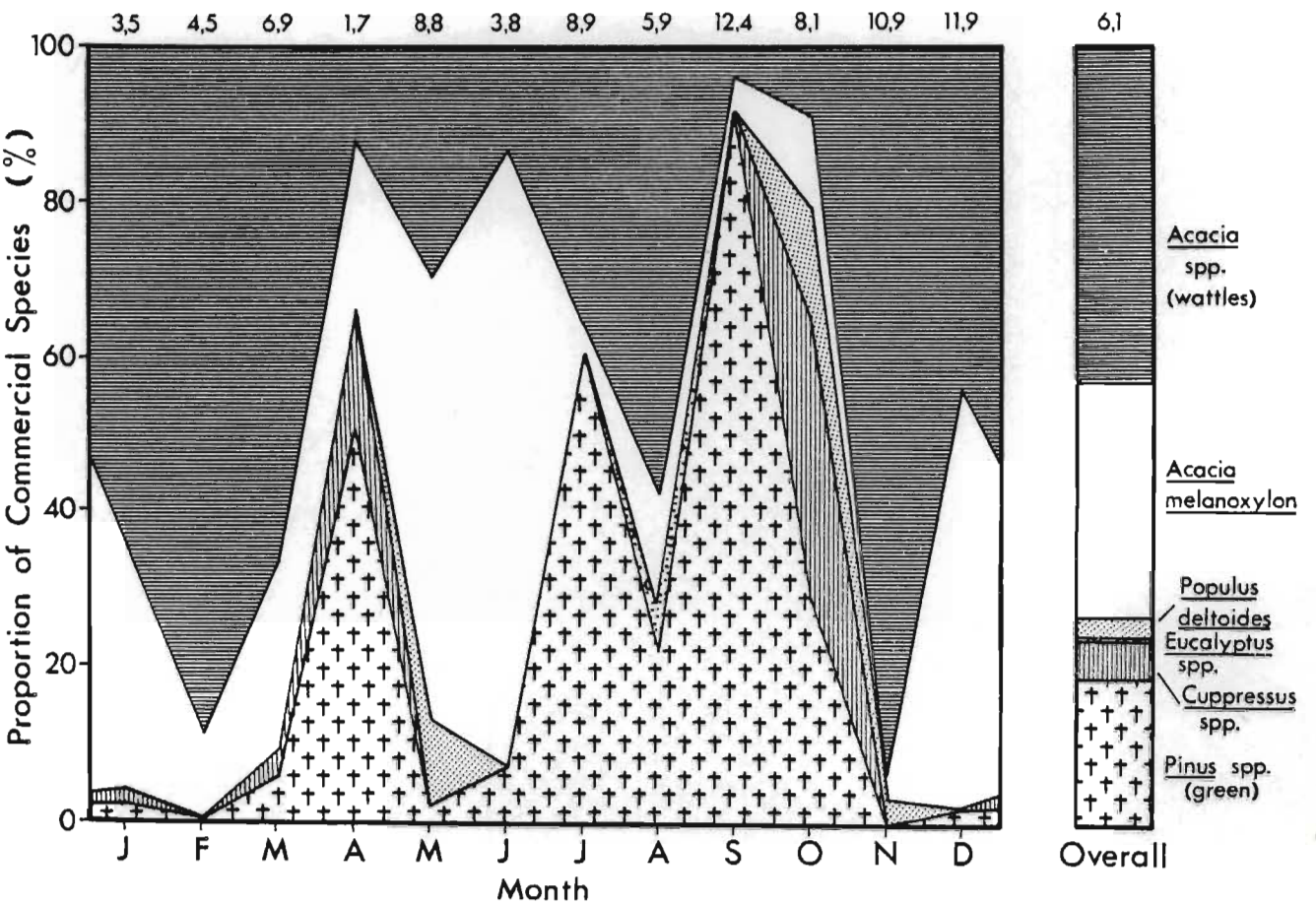


FIGURE 6.12 Monthly variation in the proportions (aggregate volume) of commercial species eaten by duiker in Weza State Forest. (Values at the top of the figure show the monthly contributions of all commercial species to the total diet for that period).

Two species of wattle (*Acacia mearnsii* and *A. dealbata*) together comprised 43,0% of the total annual volume of commercial species eaten. *Acacia melanoxylon*, *Pinus* spp. *Cuppressus* spp., *Populus detoides* and *Eucalyptus* spp.

followed in decreasing order, by volume (Fig. 6.12). Seasonally, wattles remained the dominant commercial species in the diet except in spring, when duiker utilized greater quantities of pine needles. Blackwood was the second most important timber species during summer and autumn, but was replaced by green pine during the winter, and was utilized less than pine, wattles, cypress and poplar during the spring. Green pine accounted for over 90% of the timber species eaten in September, when more quantities of commercial browse were eaten than at any other time of the year (Fig. 6.12).

b) Bushbuck

The proportion of browse from timber species found in bushbuck rumens throughout the year was more than double (13,4%) that eaten by duiker, and was eaten in greatest (17,3%) and least (5,0%) quantities during winter and summer respectively. The monthly proportions of browse from these commercial species ranged from 1,5% in November to 39,9% in August (Fig. 6.13).

Acacia melanoxylon was eaten in greater quantities than any other timber species, and accounted for 54,4% of the annual volume of commercial species consumed. Other important trees included Eucalyptus spp. (24,7%) and wattles (12,8%) while green pine needles contributed a mere 2,6% of the volume of commercial plants that were browsed (Fig. 6.13). Blackwood was the principal commercial browse during autumn and winter, but gums ranked first during spring and poplar and wattle were utilized more in the summer months (Fig. 6.13). As with duiker, bushbuck primarily ate pine needles during the spring, but apart from a small quantity utilized in July, pines were not utilized by bushbuck at any other time of the year (Fig. 6.13).

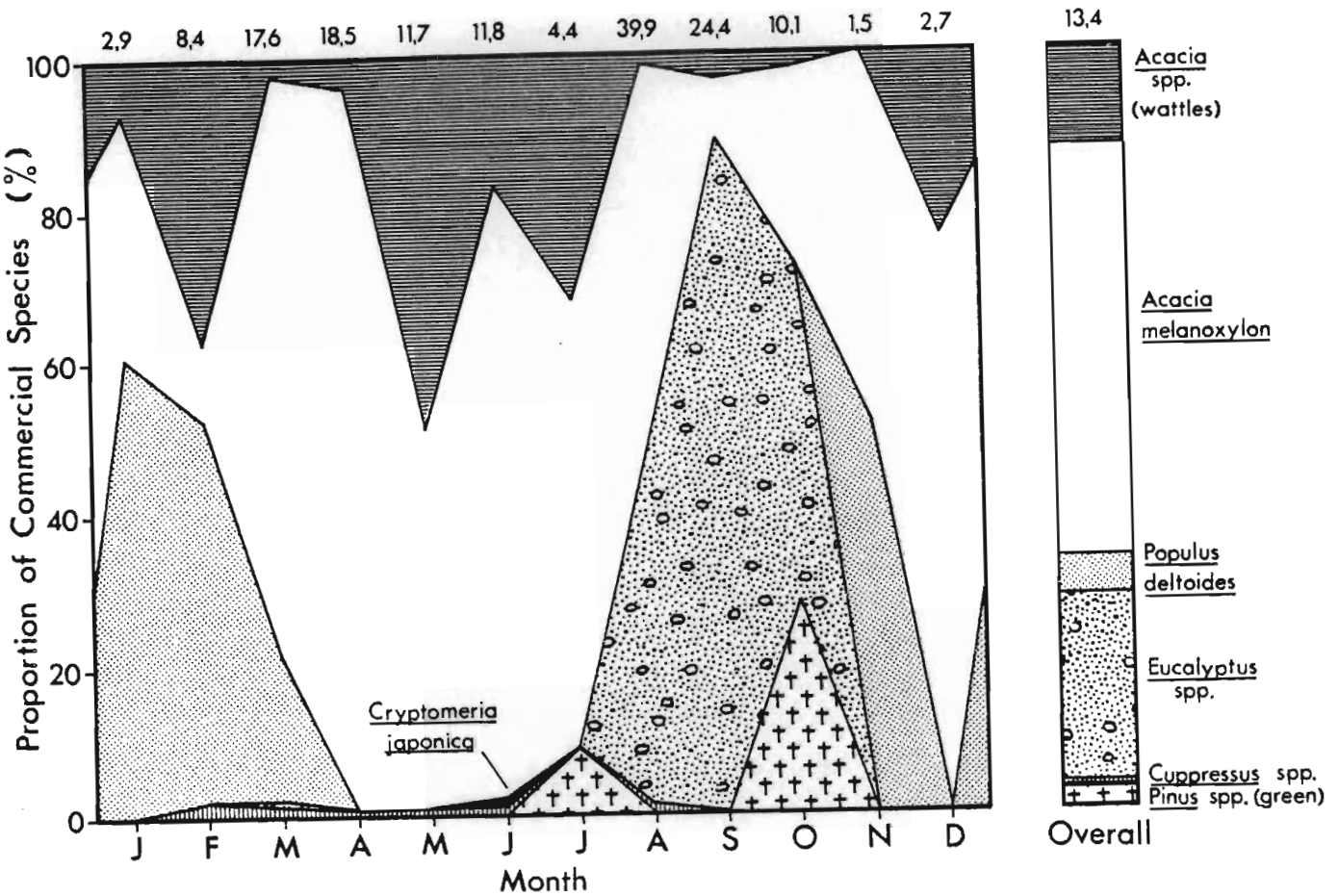


FIGURE 6.13 Monthly variation in the proportions (aggregate volume) of commercial species eaten by bushbuck in Weza State Forest. (Values at the top of the figure show the monthly contributions of all commercial species to the total diet for that period).

6.3.1.7 Diets of animals shot on neighbouring farms

a) Duiker

Rumen contents totalling 1 973,65 ml were collected from 25 duiker (average volume = 78,95 ml) shot on farms adjacent to Weza State Forest during the hunting season (31st May to 31st August). The proportion of browse eaten by farm duiker was similar to that consumed by duiker at Weza during the winter months (18,5% and 16.5% respectively), but farm duiker ate considerably more fruits and seeds, and less fungi, at this time (Fig. 6.14). The proportions of plant parts eaten

by these two populations yielded a similarity index of 69,8%.

Twenty-two plant species were identified from farm duiker rumens, and these together with sap and bark from unidentified trees amounted to 1 790,70 ml or 90,7% of the total volume. Maize (Zea mays) was the most important species by volume, while wattles were consumed more frequently than any other species, and bugweed formed the most important contribution to the diet of farmland duiker (Table 6.3). Of the remaining foods only fungi, Physalis peruviana and Pellaea viridis had % PFI values exceeding 1,0% (Table 6.3). Based on the % PFI values of all plant species eaten, the overall index of similarity in the diets of Weza and farm duiker was 50,6%.

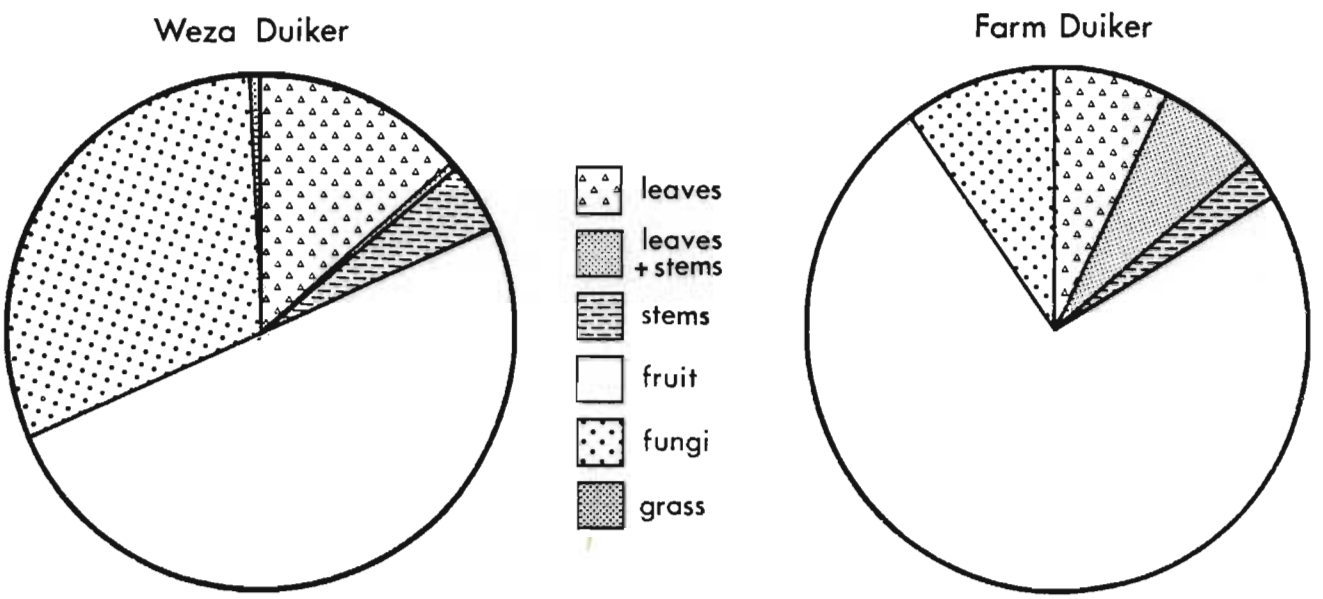


FIGURE 6.14 The proportion of plant parts eaten by duiker from Weza (n=27) and from neighbouring farms (n=25) during winter.

b) Bushbuck

A total volume of 2 030,95 ml of rumen contents were collected from 58 farm bushbuck (average volume = 35,02 ml), of which 704,05 ml (34,7%) could be identified. Bushbuck shot on these farms consumed less leaves, but more leaves and

TABLE 6.3 The winter diet of farmland duiker as determined by rumen content analysis. (Species are listed in order of decreasing PFI values, or where these are identical, in order of decreasing volume).

Species	% Volume	Frequency Index	PFI	% PFI
Solanum mauritianum	30,04	0,64	19,23	36,4
Zea mays	35,70	0,40	14,28	27,1
Unidentified	9,27	0,96	8,90	16,9
Fungi	9,63	0,40	3,85	7,3
Acacia mearnsii/A.dealbata	2,89	0,96	2,77	5,3
Pellaea viridis	1,74	0,84	1,46	2,8
Physalis peruviana	2,74	0,44	1,21	2,3
Pinus spp. (green)	1,20	0,32	0,38	0,7
Solanum aculeastrum	0,89	0,32	0,28	0,5
Solanum tuberosum	1,29	0,08	0,10	0,2
Quercus robur	1,47	0,04	0,06	0,1
Acacia melanoxylon	0,49	0,12	0,06	0,1
Phytolacca heptandra	1,11	0,04	0,04	0,1
Rubus cunifolia	0,18	0,24	0,04	0,1
Sap	0,32	0,12	0,04	0,1
Halleria lucida	0,24	0,16	0,04	0,1
Bark	0,35	0,04	0,01	tr.*
Momordica foetida	0,33	0,04	0,01	tr.
Acalypha punctata	tr.	0,04	0,00	tr.
Phaseolus vulgaris	tr.	0,04	0,00	tr.
Prunus persica	tr.	0,04	0,00	tr.
Grasses	tr.	0,40	0,00	tr.
Pinus spp. (brown)	tr.	0,08	0,00	tr.
Bidens biternata	tr.	0,08	0,00	tr.
Pteridium aquilinum	tr.	0,04	0,00	tr.

* - tr. indicates trace, i.e. < 0,01%

stems than the population at Weza, and the total proportions of browse were similar for both groups (78,4% and 75,1% respectively). Although farm bushbuck also ate greater

quantities of fungi and grass (Fig. 6.15), comparisons between the plant parts eaten in the two areas revealed a similarity index of 87,4%.

A total of 21 species formed the identified volume of 34,7% of which bugweed fruits, grass, fungi, wattles and Mexican hawthorn fruits were eaten in greatest quantities, while grass and Pellaea viridis were the species most frequently consumed. Principal foods most important to farm bushbuck were grass followed by bugweed, wattles and Pellaea viridis (Table 6.4). The high proportions of unidentified foods found in rumens from both Weza and farm bushbuck precluded any meaningful comparisons between these populations, but hunted bushbuck and duiker had a diet overlap of 11,5%. This was slightly higher than the corresponding value for bushbuck and duiker culled at Weza during the winter months (7,1%), but similar to the diet overlap of these two species throughout the year at Weza (11,7%).

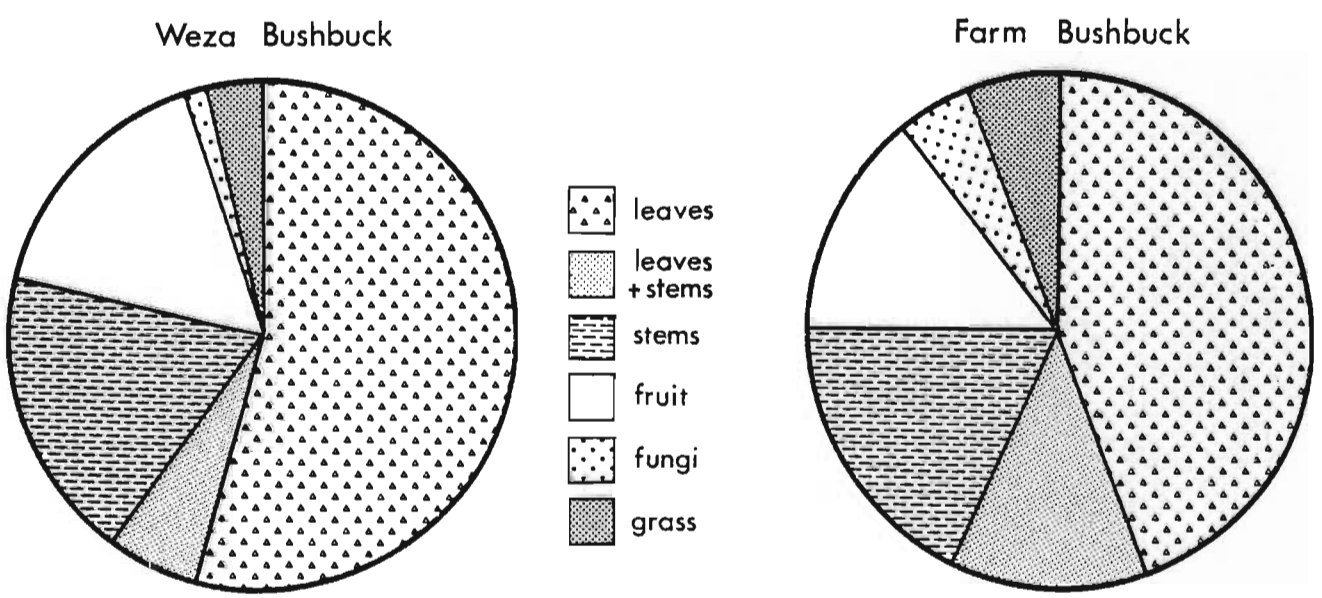


FIGURE 6.15 The proportion of plant parts eaten by bushbuck from Weza (n=31) and from neighbouring farms (n=58) during winter.

TABLE 6.4 The winter diet of farmland bushbuck as determined by rumen content analysis. (Species are listed in order of decreasing PFI values, or where these are identical, in order of decreasing volume).

Species	% Volume	Frequency Index	PFI	% PFI
Unidentified	65,33	1,00	65,33	82,2
Grasses	5,88	0,81	4,76	6,0
Solanum mauritianum	8,40	0,50	4,20	5,3
Acacia mearnsii/A.dealbata	4,58	0,64	2,93	3,7
Pellaea viridis	1,30	0,81	1,05	1,3
Fungi	4,73	0,07	0,33	0,4
Crataegus pubescens	4,19	0,05	0,21	0,3
Halleria lucida	1,06	0,16	0,17	0,2
Rubus cunifolia	0,58	0,28	0,16	0,2
Physalis peruviana	1,00	0,14	0,14	0,2
Pinus spp. (green)	0,63	0,19	0,12	0,2
Solanum aculeastrum	0,48	0,17	0,08	0,1
Raphanus sativus	0,98	0,07	0,07	tr.*
Acacia melanoxylon	0,24	0,17	0,04	tr.
Pinus spp. (brown)	0,15	0,29	0,04	tr.
Quercus robur	0,15	0,03	0,01	tr.
Phytolacca heptandra	0,14	0,03	0,00	tr.
Phaseolus vulgaris	tr.	0,03	0,00	tr.
Cotoneaster pannosa	tr.	0,02	0,00	tr.
Grewia occidentalis	tr.	0,02	0,00	tr.
Bidens biternata	tr.	0,10	0,00	tr.
Leucosidea sericea	tr.	0,02	0,00	tr.

* - tr. indicates trace, i.e. < 0,01%

6.3.2 Utilization of Commercial Species

6.3.2.1 Pines

A total of 2 200 pine seedlings in thirteen compartments were monitored during the initial survey of antelope browsing

on timber species in 1980 and 1981. These included 200 Pinus patula, 900 P. taeda and 1 100 P. elliottii seedlings (few compartments were planted with P. patula at this time.) There was no evidence of recent browsing on any of the pines planted in 1979 (n=400), and following the initial inspection in December 1980, no further browsing could be detected during the subsequent examinations in January, April and August of the following year. Similarly, pines planted in 1980 were not further utilized during January and April, but three compartments had been recently browsed by antelope when monitored in August 1981. The following results are based on the highest level of utilization each of these compartments received.

Ninety-seven (4,4%) pines were utilized to some degree during this period. More P. taeda seedlings (6,3%) were browsed than either P. elliottii (3,1%) or P. patula (3.0%). However, the vegetational state of the compartment was clearly related to browsing pressure, with only 1,4% of all pines utilized in clearfelled areas, but 14,6% of seedlings consumed to some extent in grassland areas planted for the first time.

Although only needles had been eaten from 35 (44%) of these browsed pines, the terminal shoot and needles were more frequently consumed (56%) by bushbuck and/or duiker. The calculated degree of overall utilization determined by the browsed-class method was however extremely light at 1,04% (Table 6.5).

Results from these preliminary surveys indicated that browsing on pines largely occurred during the winter and early spring months; food preference studies conducted in 1981 confirmed this (see 6.3.3). Further, the level of browsing by bushbuck and duiker was considered to be so low (98,1% of all examined pines were utilized at levels of less than 11%), when compared to other commercial species (see 6.3.2.3 and 6.3.3) that the additional time and expense involved in assessing the degree of utilization was not warranted. Consequently, all subsequent monitoring was

conducted during the winter and early spring months, and with two exceptions did not include quantitative measurements but was confined merely to the presence or absence of browsing on individual plants within each of the prescribed transects.

TABLE 6.5 Utilization of pines monitored during preliminary surveys at Weza in 1980 and 1981.

Median browsed-class (decimal value)	No.browsed seedlings	% of browsed seedlings	% current use
0,00	2103	95,6	0,00
0,055	54	2,9	0,14
0,18	12	0,5	0,09
0,38	16	0,7	0,27
0,63	7	0,3	0,19
0,83	6	0,3	0,25
0,95	2	0,1	0,10
1,00	0	0,0	0,00
Total	2200	100,0	1,04

Four additional compartments were monitored during the winter of 1981, where 1 150 plants were examined in June and again in October. Two compartments were included as a result of foresters' reports of excessive damage. In one of these, 102 of the 200 P. taeda seedlings (51%) had been utilized in a clearfelled area. However, there had been a shortage of suitably sized seedlings in the nursery at the time of planting (summer 1980) and extremely small pines (mean height of 8,6 cm) had been used. These results suggest that the younger the pine, the more susceptible it is to browsing, but once over one year of age, it is unlikely to be consumed even though it is still within the reach of a foraging duiker or bushbuck. The other compartment Forestry personnel were concerned with had 51,3% of the 400 P. elliottii seedlings browsed. The compartment had been planted for the first time, and was entirely surrounded by mature pines. This high incidence of browsing prompted further transects in another

grassland compartment surrounded by mature trees. A total of 130 P. elliottii (37%) seedlings had been browsed in this second area. The fourth compartment surveyed in 1981 consisted of a clearfelled area that had been cleaned of all weeds and other undesirable plants during the winter. Here 77 of the 200 P. elliottii seedlings were browsed during the winter.

Several trends emerged from these surveys. Firstly, the data indicated that pines in grassland were more vulnerable to browsing than those planted in clearfelled areas. Since grassland is a more preferred habitat of duiker than bushbuck, (see Chapter Seven), these results suggest the former species may be responsible for much of the damage that is caused. Secondly, pine utilization appeared to be inversely related to the local availability of alternative food resources, which would be minimal in cleaned compartments or in grassland during the winter. Eight additional compartments were therefore examined in 1982 in order to test the validity of these assumptions, although time constraints precluded the quantitative measurements of alternative foods in these areas.

Four compartments were monitored in areas known to contain relatively high densities of bushbuck but not duiker. Two of these were grasslands adjacent to large stands of indigenous forest; slight utilization of pines (3,0%, n=200) occurred in only one compartment. In addition, none of the 300 pines monitored were browsed in a third area, part of which had previously been a wattle thicket and the remaining vegetation was grassland, also adjacent to a substantial natural forest. The fourth compartment had been clearfelled the previous year and had riverine bush running along the one boundary. Pine utilization in this area where bushbuck were frequently seen at night was 1,0% in July and 4,0% in November 1982. Another clearfelled area inhabited by both bushbuck and duiker had a river running through the centre. Half the compartment to the north of the river was cleaned in June 1982 while weeds continued to flourish in the southern half. Twelve percent of the 100 trees surveyed in the

northern section had been browsed by November, while there was no evidence of damage to any of the 100 pines in the untouched section of the compartment.

The remaining three compartments all occurred in Study Area 2, where duiker were known to be abundant. The proportion of browsed pines in one afforested area was 5,5% (n=200), but 54% of all pines examined were either dead or dying as a result of damage to the bark caused by gnawing rodents. The proportion of seedlings not damaged by rodents but browsed by antelope was therefore 11,9%. The second compartment consisted of grassland and an area that had previously been a wattle thicket. The proportion of pines utilized in this compartment was 29% (n=200) in July but had increased to 41% by November. The incidence of browsing on pines in an adjacent compartment (also grassland but which had contained dense patches of bramble) was 15% (n=400) in June but when two transects each of 100 plants were re-examined in November, this had increased to 29,5%.

It should be noted that surveys in 12 of the 25 compartments, involving 2 750 pine seedlings (i.e. 55,6% of all pines examined) were not conducted at random, but were selected either because of the high incidence of utilization or in order to test predictions regarding the susceptibility of pine seedlings to browsing. Consequently, the inclusion of results obtained from these later surveys with those done initially would overestimate the incidence of browsing at Weza. Nevertheless, the combined results indicate a mean incidence of browsing of 12,6% (S.E.=3,4%). Compartments sampled for utilization surveys totalled 472,5 ha or 4,3% of the total plantation area at Weza. This is larger than the average total area reforested and afforested by Forestry staff each year.

Initial attempts to study the effects of browsing on the subsequent growth of pine seedlings were limited by grossly unequal sample sizes of browsed and intact plants in the preliminary surveys. However, the growth of browsed and intact pines was monitored in two of the four compartments

surveyed in 1981, both of which were grassland areas surrounded by mature trees. Two transects were monitored in the first area and four in the second compartment. Plants that had not been browsed but that were dying, had died, or had been replaced by Forestry staff were ignored. The proportions of browsed and intact trees that were measured in June 1982 therefore did not correspond to the initial proportions of utilized and intact plants. Results from these surveys are presented in Table 6.6 and indicate that the mean heights of browsed plants ranged from 85% to 99% of the mean heights of intact pines, when trees were measured approximately one year after browsing had occurred.

TABLE 6.6 Mean heights (cm) of browsed and intact pines in two compartments at Weza. (Utilization surveys were conducted in November 1981, heights were measured in June 1982).

	Site number					
	1a	1b	1c*	1d*	2a	2b
No. of browsed pines	37	41	43	46	41	24
No. of intact pines	43	19	18	20	31	72
Incidence of browsing (%)	46,3	68,3	70,5	69,7	56,9	25,0
$\bar{x}$ ht. of browsed pines	68,2	61,5	73,6	62,6	50,7	63,6
± S.E.	3,5	3,3	3,3	3,2	2,3	3,4
$\bar{x}$ ht. of intact pines	80,2	69,1	78,1	62,8	59,5	72,9
± S.E.	3,6	5,6	4,1	4,2	3,5	15,7
$\bar{x}$ ht. of browsed pines expressed as a % of $\bar{x}$ ht. of intact pines	85,0	89,0	94,2	99,7	85,2	87,2

* - both browsed and intact pines at these sites were extensively damaged by rodents prior to data collection in June 1982.

Additional damage caused by rodents prevented subsequent measurements in the first compartment (Site 1) but measurements of browsed and intact trees in the second compartment were again recorded in December 1984. At Site 2a, trees browsed in 1981 were on average 101,7% the height of their intact counterparts (mean = 369,5 cm, S.E.= 14,18 cm, n = 41; and mean = 365,6 cm, S.E.= 17,7 cm, n = 31 respectively). Similar results were obtained at Site 2b, where browsed pines were on average 98,5% of the height of intact specimens (mean = 373,5 cm, S.E.= 17,7 cm, n = 24; and mean = 379,4 cm, S.E.= 9,32 cm, n = 72 respectively). These results therefore indicate that browsed plants cannot be distinguished by height from intact trees in the same compartment three years after utilization. Further, with the exception of the very small seedlings planted by Forestry staff, browsing by antelope did not cause the death of any of the pines that were re-examined in this study.

6.3.2.2 Poplars

Poplar was the only other timber species of commercial value that was actively planted during the course of this study. Estimates of current utilization were facilitated by the distinction between current and old growth in this deciduous species. Three different age classes of poplar were monitored at the poplar nursery (an unprotected area of approximately 1 ha) while a fourth transect was conducted in a compartment which Forestry staff had surrounded by an electric fence. Although these fenced poplars were taller than individuals at the nursery, their inclusion was designed to test the efficacy of the electric fence in reducing damage, and therefore potentially to serve as a control. While none of the 100 monitored plants within the fenced area were browsed during the 1980-1981 growing season, the fence was discovered in an inoperative state on two occasions, while bushbuck were frequently seen inside the fenced area during late autumn and winter, particularly at night but also on three occasions during the day. Attempts to survey the

level of utilization in this fenced area were abandoned in June since many of the trees had been inadvertently slashed by Forestry labourers during cleaning operations.

Results from poplars monitored at the nursery (n = 300) indicated that smaller plants were more vulnerable and susceptible to damage from browsing than older poplars. This was particularly evident in comparisons between utilization levels of previous and current growth (Table 6.7). Further, current utilization of all three classes of poplar was light during spring, absent during summer and autumn, but increased notably during early winter. Unfortunately, Forestry staff

TABLE 6.7 Antelope utilization of poplars at Weza during 1980 and 1981

	Period monitored	Site number			
		1a	1b	1c	2
Mean height (cm)	Dec.'80	17,8	32,6	96,1	160,9
± S.E.		0,9	1,5	4,6	5,5
% of trees browsed in previous season	Dec.'80	N/A*	58,0	88,0	78,0
Previous utilization (%)	Dec.'80	N/A	36,4	38,0	26,4
% of trees browsed in current season	Dec.'80	7,0	2,0	6,0	0,0
Current utilization (%)	Dec.'80	1,5	1,3	1,3	0,0
% of trees browsed	Apr.'81	0,0	0,0	0,0	0,0
Current utilization (%)	Apr.'81	0,0	0,0	0,0	0,0
% of trees browsed	Jun.'81	16,0	4,0	12,0	N/A
Current utilization (%)	Jun.'81	6,3	2,5	3,0	N/A
% of trees browsed	Jul.'81	23,0	10,0	N/A	N/A
Current utilization (%)	Jul.'81	9,3	3,3	N/A	N/A

*N/A - indicates not available for utilization assessment.

removed the oldest class of poplars during July 1981 for replanting elsewhere, and the intermediate class were removed the following month. As with the fenced poplars, the smallest poplars at site 1a were damaged by labourers during cleaning operations. Consequently, the full extent of winter utilization by bushbuck and duiker on this species could not be assessed. Further, the survey could not be repeated as poplars were no longer considered commercially viable at Weza (J.T. Nel, pers. comm.) and the nursery area was ploughed up and planted with potatoes.

6.3.2.3 Other species

Two other transects were surveyed in 1980. The first of these consisted of 100 regenerating wattles encountered during a pine survey in a clearfelled area. Thirty percent of all wattles monitored had been browsed, and the current level of utilization was estimated at 7,0%. The other transect, also in a clearfelled area, was planted with camphor (Cinnamomum camphora), and 92% of these trees had been browsed at a level estimated at 17,7%. Since neither of these species was commercially important at Weza, the surveys were not continued, but both species were represented in the food preference trials which commenced the following year.

6.3.3 Food Preferences of Bushbuck and Duiker Feeding on Exotic Timber Species

Results concerning the extent and duration of damage caused to timber seedlings obtained from utilization surveys indicated that pines were largely browsed when few other food resources were available. The two food preference plots were designed to test this assumption further, and to determine which of the nine species available at each plot were the most preferred foods of these antelope. Although utilization by each ungulate could not be assessed separately, duiker were seldom seen in the vicinity of the first preference plot at Scylla Bridge (see Plates 4a and 4b), while bushbuck were

frequently observed in the area at night. Numerous duiker and bushbuck were seen throughout the year in the area surrounding the second preference plot, at Redlands, which was situated within Intensive Study Area 2.

For convenience, data from these two plots are summarised in Tables 6.8 and 6.9 (Scylla Bridge and Redlands respectively) as mean levels of utilization for each month they were surveyed. (These values are identical to those obtained using Schmutz's (1983) browsed-class method, but contain additional data regarding the degree of variation during each sampling period). Differences in the incidence of utilization of the various species were not significant at Scylla Bridge, but were at Redlands (X^2 = 139,9; df = 72; p<0,001) where the overall level of browsing was considerably higher. None of the pines (see Plate 4c) were consumed during the study period at Scylla Bridge, while individuals of the most utilized species, pin oak, were eaten during every month they were in leaf except in November. None of the 90 plants on offer were utilized during this month. On an annual basis, wattles (see Plate 4d) were utilized more than poplars, which in turn were eaten in greater quantities than camphors, gums, or liquidambars. As at Scylla Bridge, the preference plot at Redlands was utilized more in April-May than during any other period and was little used during late spring and summer. Pin oaks were also the most heavily utilized species in this plot, followed by wattles, camphors, gums (all of which were most utilized in autumn and winter), and then poplars. Liquidambars were the least utilized species, although these together with pin oaks and poplars were not monitored during the winter months after leaf abscission. On an annual basis, slash pines were utilized to a greater extent than either of the other pine species, and were also eaten over a longer interval. As a group, pines were not eaten before May or after November, and they were most heavily utilized during the period from August to October.

These plots were not monitored after March 1982 because several of the plants had grown beyond the reach of foraging

PLATE 4a The food preference plot at Scylla Bridge, Weza in June 1981.

PLATE 4b The food preference plot at Scylla Bridge, Weza in June 1984.

TABLE 6.8 Monthly mean levels of utilization by antelope on nine exotic timber species at Scylla Bridge, Weza, during 1981 and 1982.

Species	Monthly mean level of utilization (%) ± S.E.									
	Apr	May	Jun	Jul	Aug	Oct	Nov	Jan	Mar	ALL
Pin oak (Quercus robur)	3,5 1,8	13,2 5,7	N/A* -	N/A -	N/A -	N/A -	0,0 0,0	2,9 1,8	5,1 1,7	4,9 1,4
Liquidambar (L. styraciflua)	0,6 0,6	0,6 0,6	N/A -	N/A -	N/A -	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,2 0,1
Poplar (Populus deltoides)	4,0 1,8	7,6 5,1	N/A -	N/A -	N/A -	3,8 3,8	0,0 0,0	0,0 0,0	0,0 0,0	2,2 0,9
Camphor (Cinnamomum camphora)	0,6 0,6	0,6 0,6	1,8 1,8	0,6 0,6	4,4 3,8	7,6 5,1	0,0 0,0	0,0 0,0	0,6 0,6	1,8 0,8
Wattle (Acacia spp.)	0,6 0,6	4,0 2,7	13,7 10,9	2,3 2,3	2,3 2,3	0,0 0,0	0,0 0,0	0,7 0,7	0,0 0,0	2,8 1,4
Gum (Eucalyptus sp.)	0,0 0,0	0,0 0,0	0,0 0,0	6,3 6,3	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,7 0,7
Loblolly pine (Pinus taeda)	0,0 0,00	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0
Patula pine (Pinus patula)	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0
Slash pine (Pinus elliottii)	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0
No. of species browsed	5	5	2	3	2	2	0	2	2	6
$\bar{x}$ level of utilization	1,0	2,9	2,6	1,5	1,1	1,4	0,0	0,4	0,6	1,4
± S.E.	0,5	1,6	2,2	1,0	0,8	1,0	0,0	0,3	0,6	0,6

* N/A - not available or monitored; deciduous species.

bushbuck and duiker, thus hindering assessment regarding the availability of each species. The widely divergent levels of utilization in each area prompted attempts to establish duplicate plots in other areas, but these were unsuccessful due to a shortage of certain stocks in the Forestry nursery. Both original plots were revisited in June 1984, but no attempts were made to assess levels of utilization because of differential growth rates and because I was no longer familiar with the growth form of individual plants. Nevertheless, utilization of all species except pines at the

TABLE 6.9 Monthly mean levels of utilization by antelope on nine exotic timber species at Redlands, Weza, during 1981 and 1982.

Species	Monthly mean level of utilization (%) ± S.E.									
	Apr	May	Jun	Jul	Aug	Oct	Nov	Jan	Mar	ALL
Pin oak (*Quercus robur*)	83,8 3,9	96,0 0,7	N/A* -	N/A -	N/A -	N/A -	39,3 13,2	19,9 7,0	34,0 9,3	54,1 5,5
Liquidambar (*L. styraciflua*)	2,9 1,8	0,6 0,6	N/A -	N/A -	N/A -	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,6 0,3
Poplar (*Populus deltoides*)	0,0 0,0	0,0 0,0	N/A -	N/A -	N/A -	16,7 16,7	0,0 0,0	10,5 10,5	0,0 0,0	4,2 3,0
Camphor (*Cinnamomum camphora*)	5,5 3,7	17,3 9,9	12,9 4,7	16,7 6,9	12,5 5,6	12,5 6,9	0,6 0,6	1,1 0,7	1,1 0,7	8,9 1,8
Wattle (*Acacia* spp.)	22,9 7,2	60,7 15,6	23,4 8,5	33,0 11,3	46,3 19,2	42,2 22,5	0,0 0,0	0,0 0,0	18,8 8,5	25,1 4,1
Gum (*Eucalyptus* sp.)	0,9 0,9	10,2 6,1	6,1 4,6	21,3 12,6	9,5 9,5	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	5,9 2,1
Loblolly pine (*Pinus taeda*)	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	7,2 3,8	5,6 3,6	0,0 0,0	0,0 0,0	0,0 0,0	1,4 0,6
Patula pine (*Pinus patula*)	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	0,0 0,0	3,8 3,8	7,6 5,1	0,0 0,0	0,0 0,0	1,3 0,7
Slash pine (*Pinus elliottii*)	0,0 0,0	0,0 0,0	3,8 3,8	7,4 4,1	5,6 4,0	3,6 2,4	0,0 0,0	0,0 0,0	0,0 0,0	2,3 0,8
No. of species browsed	5	5	4	4	5	6	3	3	3	9
$\bar{x}$ level of utilization	12,9	20,5	7,7	13,1	13,5	10,6	5,3	3,5	6,0	11,5
± S.E.	9,2	11,5	3,7	5,3	6,8	5,0	4,3	2,3	4,1	5,9

* N/A - not available or monitored; deciduous species.

Scylla Bridge plot appeared to have increased substantially (see Plates 4a and 4b). This may have resulted from the considerable changes in the surrounding habitats, where large stands of mature pines had been felled, although whether this had affected the local densities and distributions of bushbuck and duiker is not known. Forestry staff planted the area surrounding and including the Redlands plot with *P. taeda* in April 1982, and none of the camphors, wattles or gums remained in 1984. Since all of the pin oaks were still growing, it is probable that the missing species had been

PLATE 4c An intact 3,5 year old patula pine (Pinus patula) at the Scylla Bridge preference plot. (Photograph taken in June 1984; height of range rod = 2,5m).

PLATE 4d A heavily browsed 3,5 year old wattle (Acacia sp.) at the Scylla Bridge preference plot. (Photograph taken in June 1984; scale on card = 10cm).

removed by Forestry staff. More than 50% of the original pines planted in the preference plot had been damaged by rodents and several of these were either dying or had died. A random survey of the younger pines (n = 100) within this compartment revealed that 97% suffered from bark removal by rodents.

6.4 DISCUSSION

As stated in the Introduction, the full implication of the results emanating from this aspect of the study should not be considered in isolation. Consequently, attention in this discussion is centred on those aspects that are pertinent to an understanding of the feeding ecology of bushbuck and duiker; factors related to habitat requirements and management strategies are considered in Chapters Seven and Ten.

6.4.1 Rumen Analysis

As a result of their large surface area/volume ratio, small ungulates have much higher metabolic requirements in relation to their body size than larger species (Kleiber 1961; Owen-Smith 1982; Coe 1983). In order to fulfil these requirements, small ungulates tend to select for highly nutritious food that is both more soluble and digestible than the diets of larger species (Bell 1970; Jarman 1974; Schwartz and Ellis 1981). Further, those ungulates selecting for a highly nutritious diet tend to have relatively small rumens (Hofmann 1973) and low rumeno-reticular capacity relative to body mass (Hofmann and Stewart 1972; Giesecke and van Gylswyk 1975; Hoppe 1977; Owen-Smith 1982) and relatively simple rumens with few structures to impede the throughput of food (Hofmann 1973). Hofmann and Stewart's (1972) inclusion of bushbuck and duiker as selectors of juicy, concentrated herbage, particularly dicotyledon foliage, is supported by the result of this study. Both species are therefore likely

to have high fermentation rates and a rapid turnover time, with food being retained in the digestive tract for as little as 24 hours (Hoppe 1984b). This would indicate that both species, like North American deer (Short 1963), cannot digest fibrous growth rapidly enough to subsist on high fibre forages. In addition, fibrous portions of their diets are likely to be retained in their rumens for longer periods than succulent foods (see Short 1975; Demment 1982; Boomker 1983), yet both species probably eat and ruminate fairly frequently (Hoppe 1984b). Consequently differential digestion, while recognised as a major problem associated with dietary assessments (see 6.1.1.4) is likely to be exaggerated by the inclusion of small plant fragments in rumen content analyses. The possibility that the majority of the smaller fragments from rumen contents are largely fibrous foods that were eaten several meals ago does not appear to have been appreciated by several authors opposed to the use of sieves in separating different sized items of food (see 6.1.1.4). Other authors have recognised that the more succulent items of food may be under-represented in rumen analysis (Anderson et al. 1965; Nellis and Ross 1969; Mitchell and Smoliak 1971; Borowski and Kossak 1975; Jackson 1977; Gavin et al. 1984), but none have suggested that screening the rumen contents might actually increase the accuracy of the technique by removing the accumulation of coarser, fibrous material. The high proportions of large succulent items (see Plate 3) in the diets of bushbuck and duiker (which, because still intact, indicate that these had recently been eaten) together with the feeding strategies of these two species, therefore suggest that screening may well enhance rather than reduce the accuracy of this method.

6.4.1.1 Nutritional factors influencing diet selection

This study of the feeding ecology of bushbuck and duiker in a forest environment should not be regarded as exhaustive; rather it provides base-line data that should be supplemented by considerable additional research. Conclusions regarding the importance of food items or species consumed by these two

antelope species are somewhat limited by the methods of data collection and analysis. An obvious caveate concerns the high proportion of bushbuck foods that were not identified (Fig. 6.4). However, these items were not obviously abundant in the plantations and were probably from the indigenous forests, while comparisons between the diets of these two ungulates are considered valid because of the high proportion of duiker foods that were identified each month (Fig. 6,3). Little use could be made of statistical analyses in describing diets because of the intraspecific variation in both the volumes of rumen contents collected and in the quantities of specific food items consumed by individual animals. This variation is a problem common to numerous feeding studies and is probably best ameliorated by the use of %PFI (or a similar index) that incorporates both frequency and volumetric data since either of these used alone may yield rather misleading results (Suida et al. 1969; Jackson 1980). Serious omissions in this study include information regarding food preferences and quality. No attempt was made to determine preferences because of the enormous difficulties that would be encountered in estimating the availability of individual plant species occurring in a mosaic of small but highly diverse habitats. Totally erroneous conclusions regarding preferences could result from sampling the availability of plant species in areas not visited (e.g. beyond the boundaries of exclusive home ranges) by culled individuals (see 6.1.1.6) while the path of a foraging bushbuck or duiker could only be determined by radio telemetry; such animals were considered far too valuable for sacrifice. Food quality was not considered in this study due to time and financial constraints. Nevertheless, as Hanley (1982) points out: "diet composition data alone are not satisfactory for explaining the reasons for observed diet differences between animal species". In addition, an understanding of the forage needs of wildlife requires a knowledge of the reasons why certain plants are selected; only then can carrying capacities be estimated and habitats be effectively improved for intensive management (Snider and Asplund 1974; Mitchell et al. 1977; Hanley 1982; Leslie et al. 1984). Numerous factors may influence the

selection of certain plant parts or species by wildlife, including season, the botanical composition of the flora, the relative abundance of food items, ungulate densities, the nutrient quality of the forage, and the metabolic requirements of individual animals (see above and 6.1.1.6). Furthermore, plant parts or species will vary in their proportions of nutrients essential to the foraging herbivore, which must therefore select a diet from a mixture of food items of unequal nutritive value (Westoby 1978; Vangilder et al. 1982). Reasons why individual items are selected should therefore be interpreted with caution.

While the limitations of this study are recognised, comparative data are lacking since only one account of the feeding ecology of an African ungulate in a forest environment has been published and this was of short duration and was based on relatively few specimens (Odendaal 1983). In contrast, the composition and quality of the diets of forest ungulates has received considerable attention in North America and Europe. Many of these northern hemisphere studies are particularly informative since several cervids also combine a high rate of digestion with a rapid rate of passage to supply their high metabolic requirements (Snider and Asplund 1974). Furthermore, bushbuck and duiker at Weza show remarkable dietary similarities to those of northern temperate deer; as show below such similarities extend beyond the consumption of various plant parts and include numerous plants of the same genera. The results of this study, while more indicative then definitive, are therefore more meaningful when compared to other forest ungulate studies, particularly if these are detailed in conjunction with the likely benefits bushbuck and duiker derive from the foods that are consumed.

Plant cellular contents are the most valuable food source for herbivores because they are highly (approximately 98%) digestible (Hanley 1982; Vangilder et al. 1982). Because cell walls consist of cellulose, hemicellulose and lignin, these are much less digestible, particularly since cellulose digestion is a time-consuming process while lignin

is generally considered non-digestible (Goering and Van Soest 1970 cited in Hanley 1982). The most digestible forages are therefore those parts of forbs and shrubs that are actively and rapidly growing or have recently developed (e.g. leaves and new stem growth) as these generally have relatively thin cell walls and a high volume of cell contents, while mature grasses and slow-growing woody tissue are least digestible due to the high content of cellulose and lignin respectively in their thick cell walls (Short 1971, 1975; Halls and Alcaniz 1972; Segelquist et al. 1972; Blair et al. 1977). In addition, it is generally accepted that the crude protein of herbivore food is related to its nutritive value, whereas crude fibre is inversely related to it (Klein 1962). A crude protein level of 5% is considered to be the maintenance threshold for a number of ungulates (Chalmers 1961 cited in Coe 1983; Shafer 1965 cited in Morow 1977; Owen-Smith and Novellie 1982) while levels of 9-11% and 16% are required for moderate growth and maximum growth and reproduction respectively (Lockie 1967; Everitt and Gonzalez 1981). Other nutritive values of forages commonly examined are crude fat and energy. Crude fat consists of true fat and, to a greater extent, essential oils. Ruminants are not dependant on true fat which can be synthesized in the rumen from carbohydrates and proteins. The major source of energy to ungulates is from volatile fatty acids, which are derived from carbohydrate fermentation and then absorbed from the rumen (Owen-Smith 1982) and to a lesser extent from the caecum (Boomker 1983).

6.4.1.2 Plant parts and forage classes consumed by duiker and bushbuck

Since fruits and mast generally have high calorific values and are readily utilized by ungulates (Duvendeck 1962; Short et al. 1969a; Burns and Viers 1973; McCaffery et al. 1974; Snider and Asplund 1974: Short 1975; Short and Epps 1976; Johnson and Landers 1978; Landers et al. 1979; Vangilder et al. 1982) results from this study suggest that these provided a source of high energy for duiker throughout

much of the year, but particularly during the winter months (Fig. 6.5). The importance of fruits in the diets of several other wildlife species inhabiting forested regions have been noted by numerous other authors (e.g. Dunkeson 1955; Lay 1965; Nixon et al. 1970; Skinner and Telfer 1974; Stransky and Halls 1980; Servheen 1983). During the autumn and winter months duiker also consumed large quantities of fungi (Fig. 6.4) which are probably rich in protein and are very digestible (Short 1975). Duiker consumed equal and greatest quantities of browse during the spring and summer months, the majority of which was taken from trees and shrubs, although the proportion of forbs eaten increased from 6,8% in spring to 28,2% in summer (see Fig. 6.7). Possible reasons for the inclusion of large quantities of browse during spring and summer must be speculative and may simply be related to the relative availability of other food items at these times. However, it is equally feasible that foliage from trees, shrubs and forbs was actively selected since such browse would be most nutritious (in terms of protein) and palatable during this active phase of growth (see Dunkeson 1955; Chamrad and Box 1968; Nixon et al. 1970; Short 1971, 1975; Kufeld et al. 1973; McCaffery et al. 1974; Snider and Asplund 1974; Hall-Martin and Basson 1975; Blair et al. 1977; Deschamp et al. 1979; Hosey 1981; Papageorgiou et al. 1981; Crawford 1982; Kossak 1983). Grass and flowers were probably consumed for similar reason although neither of these featured dominantly in the diet of duiker at Weza (Fig. 6.5).

Although duiker at Weza consumed a high proportion of fungi and generative plant parts throughout the year, and therefore had a diet similar to that of roe deer (Jackson 1977; Kossak 1983), this was in marked contrast to the diet of bushbuck, which consisted largely of browse (89,5%, see Fig. 6.6). This browse consumption was least in winter (when it was eaten in greater quantities by duiker than at any other time of the year), but still remained dominant in the diet (78,7%). Since duiker rumen contents revealed that fruits and fungi were available for much of the year, these results suggest that bushbuck showed a preference for browse

over these other items; fruits and seeds were important only during winter while small volumes of fungi were eaten in spring (Fig. 6.6). Bushbuck also differed notably from duiker in the proportions of stems eaten throughout the year. Bushbuck at Weza are therefore more similar in dietary habits to lesser and greater kudu (Leuthold 1971a; Owen-Smith 1979; Owen-Smith et al. 1983) both of which are included in Hofmann and Stewart's (1972) category of tree and shrub foliage eaters. Whether food retention is longer in the bushbuck than the duiker, or whether bushbuck rely on rapid excretion of fibrous diets rather than prolonged digestion, as has been proposed for mule deer by Hobbs et al.(1983), is not known. The importance of browse from trees, shrubs and forbs during winter has been noted in numerous studies of northern hemisphere cervids (e.g. Martinka 1968; Bayless 1969; Healy 1971; Segelquist et al. 1972; Boeker et al. 1972; Kufeld et al. 1973; Borowski and Kossak 1975; Blair et al. 1977; Jackson 1977, 1980; Henry 1978).

Forage class data were less comprehensive from the rumens of bushbuck because of the high proportion of unidentified material, but nevertheless show close agreement with the relevant studies of this species elsewhere (Jacobsen 1974; Simpson 1974b; Okiria 1980; Odendaal 1983). Odendaal (1983) found that forbs were more frequently eaten than shrubs during the winter, and bushbuck at Weza ate more forbs in winter than at any other time of the year. These may have been eaten in the indigenous forest, or quite possibly, like grass, were removed from cut-outs and fire breaks that had been burned during the previous autumn. Grasses were eaten in greatest quantities during spring, presumably when they were most nutritious (see Allen 1968; Healy 1971; Todd 1975; Henry 1978; Martinka 1968, 1969; Dunham 1980; Korfhage et al. 1980; Rowland et al. 1983). As in Odendaal's (1983) study, ferns were little utilized by bushbuck at Weza during the winter months, but were important at other times of the year, particularly summer (Fig. 6.8). Substantial amounts of ferns have also been noted in the diets of cervids during summer and autumn (e.g. Healy 1971; Kohn and Mooty 1971; Henry 1978; Jackson 1980; Stormer and Bauer 1980; Crawford 1982).

6.4.1.3 Principal species consumed by duiker and bushbuck

On an annual basis, only eight species (including all fungi) and unidentified material eaten by duiker had %PFI values of 1% or more (Table 6.1). Only five species eaten by bushbuck had %PFI values equivalent to or exceeding 1% (Table 6.2) and these were lower values than the major duiker foods because of the high proportion of unidentified material from bushbuck rumens. The fact that changes in species utilization may have resulted from increasing availability of other more preferred species is recognised as is the possibility that individual animal diets may have been drastically altered by localised silvicultural or exploitation practices. Nevertheless, several significant trends are evident from the results of this study.

Fungi were clearly more important in the diet of duiker than any other food, were most utilized in autumn and early winter and formed at least 20% of the diet for two thirds of the year. Fungi are also highly rated foods of ungulates in the northern hemisphere (see Table 6.10). Due to their relatively low abundance and contribution to the total forage biomass (see Harlow et al. 1975; Blair et al. 1984), fungi may be considered as preferred foods of duiker. Fungi contain high levels of crude protein, phosphorus and cell solubles (Bergerud 1972; Short 1975; Blair et al. 1977; Jones and Weeks 1985) - a recent study by Blair et al. (1984) revealed monthly crude protein levels ranging from 17,8% to 31,9%, phosphorus levels of 0,31% to 0,75% (which was considerably higher than those of native forages and fruits) and dry-matter digestibility values from 52,7 to 75,4%. Harlow et al. (1975) claimed that because of the high moisture content of fungi, deer would have to consume large quantities for their dietary requirements and since fungi were seldom abundant, these could not be considered a staple food. Despite the ephemeral nature of this food, fungi clearly were of major importance to duiker at Weza, but were seldom utilized by bushbuck except in late winter and early spring, when they were probably least available. A diet

consisting largely of fungi would provide duiker with an excellent source of protein for much of the year, but particularly during autumn and late winter. This food may also have been selected for its high phosphorus content, as this mineral has been found to be inadequate in several ungulate diets and may be severely limiting in several forested habitats (Lay 1957; Lockie 1967; Dietz 1970; Halls 1970; Urness et al. 1975; Blair et al. 1977; Everitt and Gonzalez 1981).

TABLE 6.10 The importance of fungi in the diets of ungulates from the northern hemisphere.

Source	Consumer	Maximum % in diet	Importance rating	Season most utilized
Bergerud 1972	Caribou	25	-	summer
Collins et al. 1978	Elk	-	2	summer
Crawford 1982	White-tailed deer	45	1	autumn
Deschamp et al. 1979	Mule deer	21	-	summer
Dunkeson 1955	Deer	25	-	summer
Harlow et al. 1975	White-tailed deer	21	-	winter
Healy 1971	White-tailed deer	6	2	autumn
Henry 1978	Roe deer	4	-	summer/autumn
Hungerford 1970	Mule deer	-	-	late summer
Jackson 1977	Fallow deer	6	-	winter
Jackson 1980	Roe deer	7	-	winter
Kaluzinski 1982	Roe deer	4	-	autumn
Kohn & Mooty 1971	White-tailed deer	7	-	summer
Korschgen et al. 1980	White-tailed deer	6	2	spring
Nixon et al. 1970	Deer	7	-	summer
Short 1971	White-tailed deer	-	2	summer
Skinner & Telfer 1974	White-tailed deer	6	-	autumn
Thill 1984	White-tailed deer	1	-	autumn
Wood & Roark 1980	Feral hogs	12	-	summer

* 1 = most important or most preferred species in the diet.
2 = species of major importance or highly preferred in the diet.

Bramble was the second most important species eaten by duiker, and the principal item of the identified foods of bushbuck (Tables 6.1 and 6.2 respectively). Both ungulates consumed greater quantities of bramble (largely leaves, buds and young shoots) during spring than at any other time of the year (Figs. 6.9 and 6.10), but because this plant, together with bugweed, is undoubtedly the most abundant browse species in the plantation, it is highly unlikely that bushbuck and

duiker were competing for this resource. Fruits of this species were readily consumed at all stage of ripeness by duiker as they became available in the summer, but the importance of this species to bushbuck rapidly declined during summer and fruits were eaten only in January. Bramble was of negligible importance to both ungulates during winter, presumably as a result of leaf abscission and the low nutritive content of the remaining stems (see Conroy et al. 1982). Members of this genus are of considerable importance to ungulates from forested habitats in the northern hemisphere (Table 6.11) while Landers et al. (1979), Papageorgiou et al (1981) and Conroy et al. (1982) found Rubus spp. leaves and fruits to have crude protein contents ranging from 9,8 to 12,7% and gross energy values of 4,39 - 5,40 Kcal/g.

TABLE 6.11 The importance of Rubus species in the diets of herbivores in the Northern Hemisphere.

Source	Consumer	Maximum % in diet	Importance rating *	Parts eaten	Season most utilized
Bergerud 1972	Caribou	7	-	not specified	spring
Bobek et al. 1979	Roe & red deer	3	-	not specified	
Borowski & Kossak 1975	Roe & red deer	8	-	not specified	all year
Crawford 1982	White-tailed deer	10	2	leaves	autumn
Crouch 1968	Black-tailed deer	-	2	not specified	winter
Dzieciolowski 1970	Red deer	-	1	twigs	all year
Halls 1975	White-tailed deer	-	2	twigs	winter
Healy 1971	White-tailed deer	-	1	not specified	all year
Henry 1978	Roe deer	14	2	not specified	autumn
Hosey 1981	Roe deer	84	1	not specified	all year
Jackson 1977	Fallow deer	17	2	not specified	winter
Jackson 1980	Roe deer	46	1	not specified	all year
Johnson & Landers 1978	Deer	-	1	not specified	summer
Lay 1967	White-tailed deer	-	2	not specified	
Korschgen et al. 1980	White-tailed deer	7	2	fruits,leaves,twigs	summer
Kossak 1976	Roe & red deer	9	-	twigs	
Nixon et al. 1970	Deer	4	-	fruits,leaves,twigs	summer
Papageorgiou et al. 1981	Roe deer	-	2	not specified	
Puglisi et al. 1978	White-tailed deer	-	-	fruits, leaves	spring/summer
Stormer & Bauer 1980	White-tailed deer	13	2	fruits, leaves	summer
Thill 1984	White-tailed deer	3	1	not specified	summer/autumn

* 1 = Most important or most preferred species in the diet.
2 = Species of major importance or highly preferred in the diet.

Bugweed ranked third and tenth in the overall diets of duiker and bushbuck respectively (Tables 6.1 and 6.2). The stems and leaves of this abundant plant were never eaten by either antelope and may therefore be considered as an avoided or non-preferred item of the diet. Because individual trees fruited at different times, fruits were available throughout the year but were consumed in greatest quantities by both ungulates during the winter (Figs. 6.9 and 6.10). However, bugweed fruits were of much greater importance to duiker, maintaining a %PFI value of 70,7% during June (Table 6.1) but never exceeding 3% for bushbuck (Table 6.2) These fruits were presumably consumed as a result of their high calorific values and readily digestible cell contents. If undamaged seeds voided by the animal could germinate, then duiker may act significantly in the dispersal of this plant, and also possibly bramble. Both of these plants are considered as noxious weeds at Weza yet both form important structural components of preferred bushbuck and duiker habitats (see Chapter Seven).

With the exception of February (when the diet included a high proportion of unidentified food material and fruit from domestic trees) fungi, bramble and bugweed fruits constituted more than 60% of the monthly diets of duiker (Table 6.1). It may well be that these species complement each other and that duiker prefer to feed on "food blocks" (as has been suggested for roe and red deer, Borowski and Kossak 1975; Kossak 1976), rather than individual species.

Two hardwood (wattles and blackwood) and one group of softwood (pines) commercial species featured in the 10 most important food items of duiker, but only blackwood had an overall %PFI valued exceeding 1% in the diet of bushbuck. These are considered below in 6.4.1.4.

Pellaea viridis was the most important fern in the diet of duiker and bushbuck and was eaten in greatest quantities by both antelope during late summer and autumn (Tables 6.1 and 6.2). This species is particularly abundant in young plantations and in the understory of pines of intermediate

age, and was therefore probably eaten in relation to its abundance rather than constituting a preferred species.

Acorns from the oak Quercus robur were the only other food contributing an overall %PFI value of at least 1% in the diet of duiker at Weza. This mast was ranked 17th in the foods of bushbuck (Table 6.2). However, because of the extremely localised availability of oaks at Weza, acorns must be considered as a highly preferred food of both bushbuck and duiker. The most extensive stands of oaks occurred within Study Area 1, where animals were not culled. These oaks, devoid of any understory, were highly preferred nocturnal autumn and winter habitats for both antelope species (see Chapter Seven) and since they offered no cover, were presumably utilized for foraging purposes. Cursory inspections of these oak stands in late winter and spring revealed that few acorns remained in the leaf litter, and the few that did germinate were totally utilized before the onset of the following winter. Acorns were also sought after by baboons and porcupines.

Oak leaf litter was never found in rumen samples from either species, perhaps because of the low digestibility and nutritious value of fallen leaves (Segelquist et al. 1972). Korschgen (1962) considered oak leaves as a starvation food. Although Fowler and Richards (1965) cite examples of acorn and oak leaf poisoning to domestic livestock from the tannins in this genus, oaks and acorns are highly preferred foods for numerous species of wildlife in North America and Europe (see Nichol 1938, Forbes et al. 1941, Martin et al. 1951 and Lay 1957a, all cited in Goodrum et al. 1971; Ruff 1938, Pearson 1943, Pearson and Burnett 1940, Harlow 1961, Harlow and Hooper 1971 all cited in Harlow et al. 1975; Dalke 1941, Hahn 1945, Lindzey 1952 and Dexter et al. 1952 all cited in Korschgen 1962; Knierim et al. 1971; Kufeld et al. 1973; Snider and Asplund 1974; Cherry and Dearden 1975; Short 1976; Wolgast and Stout 1977 and Table 6.12).

Numerous studies have been conducted on the nutritive value of Quercus spp. Crude protein levels of browse ranged

TABLE 6.12 The importance of Quercus species in the diets of large mammals from the northern hemisphere.

Source	Consumer	Maximum % in diet	Importance rating *	Parts eaten	Season most utilized
Anderson et al. 1965	Mule deer	27	1	leaves	spring/summer
Boeker et al. 1972	Mule deer	24	2	leaves, twigs	all year
Borowski & Kossak 1975	Roe & red deer	14	-	leaves,twigs,bark	winter/summer
Coblentz 1970	White-tailed deer	9	1	leaves	winter
Della-Bianca & Johnson'65	White-tailed deer	-	2	leaves, twigs	winter
Dunkeson 1955	Deer	-	2	acorns	autumn/winter
Dzieciolowski 1970	Red deer	-	2	twigs	summer
Garshelis & Pelton 1981	Black bear	-	2	acorns	autumn
Goodrum et al. 1971	White-tailed deer	98	1	acorns	autumn
Halls & Crawford 1960	White-tailed deer	-	2	not specified	summer/winter
Harlow et al. 1975	White-tailed deer	76	1	leaves, acorns	autumn/winter
Holl et al. 1979	Mule deer	-	2	leaves, twigs	winter
Hosey 1981	Roe deer	46	2	not specified	summer
Hubert et al. 1980	White-tailed deer	27	-	acorns	autumn
Jackson 1977	Fallow deer	32	2	acorns	autumn
Jackson 1980	Roe deer	14	2	acorns	autumn
Kaluzinski 1982	Roe deer	9	2	leaves, twigs	spring
Korschgen 1962	White-tailed deer	80	1	leaves, acorns	autumn/winter
Korschgen et al. 1980	White-tailed deer	5	2	acorns	late summer
Krausman 1978	White-tailed deer	11	2	not specified	late summer
Landers et al. 1979	Black bear	17	2	acorns	autumn
Maehr & Brady 1984	Black bear	29	2	acorns	autumn/winter
McCaffery et al. 1974	White-tailed deer	14	2	acorns	autumn
Nixon et al. 1970	Deer	20	2	leaves, acorns	autumn/winter
Puglisi et al. 1978	White-tailed deer	-	2	leaves, acorns	summer/autumn
Segelquist & Green 1968	Deer	-	1	acorns	winter
Segelquist et al. 1972	White-tailed deer	16	-	acorns	winter
Short et al. 1969a	White-tailed deer	93	-	acorns	autumn
Short 1971	White-tailed deer	75	2	acorns	autumn
Szukiel 1981	Deer	-	2	twigs	winter
Wood & Roark 1980	Feral hogs	80	1	acorns	winter

* 1 = Most important or most preferred species in the diet.
2 = Species of major importance or highly preferred in the diet.

from 4,3% for twigs to 14.8% for leaves, while gross energy values were from 4,8 to 5,1 Kcal/g respectively (Papageorgiou 1978a; Papageorgiou et al. 1981; Conroy et al. 1982). Chemical analyses of acorns have shown these to be rich in crude fat and relatively low in crude fibre and moisture content, making them readily digestible, concentrated sources of energy (Burns and Viers 1973; Short 1975; Short and Epps 1976; Landers et al. 1979). However, acorns have a low protein content of approximately 6% as well as a low phosphorus level (Short et al. 1969a; Short 1976; Short and

Epps 1976; Landers et al. 1979; Reid and Goodrum 1979) and as Short and Epps (1976) point out "their consumption should not be expected to alleviate protein deficiencies encountered from eating other forages during autumn and winter". Nevertheless, this palatable and highly digestible food clearly provides a rich source of carbohydrate at times when other quality foods are uncommon and may be particularly important in fat deposition during the autumn and winter months (McCaffery et al. 1974). Dunkeson (1955) noted that the yields from annual acorn crops had a marked effect on the amount of browsing on other winter foods, and found that damage to pines and other non-preferred conifers was most severe in years when acorns were scarce. Korschgen (1962) also recorded an increased use of evergreen browse and agricultural crops during mast shortages, and Crawford and Leonard (1963) cited in Segelquist and Pennington (1968), Segelquist and Green (1968) and Harlow et al. (1975) reported a similar inverse relation between acorn yields and browse utilization. At a more extreme level, Segelquist et al. (1969) found that severe mortality of white-tailed deer occurred during two winters out of five when acorn yields were lowest. Deer losses were much lower and never exceeded production in a neighbouring area where mast and forage were more abundant.

6.4.1.4 Commercial species consumed by duiker and bushbuck

Duiker utilization of commercially important timber species remained relatively constant throughout the year (Fig. 6.9) although there were marked seasonal differences in the species that were consumed (Fig. 6.12.). In contrast, bushbuck showed an increase in the use of timber species during autumn, winter (particularly August) and early spring (Fig. 6.10) but showed similar trends in the seasonal use of individual species.

Wattles and blackwood (Acacia spp.) were the most important timber species in terms of their contributions as

duiker foods and ranked fifth and sixth respectively in the overall diet. Both of these species had overall %PFI values exceeding 1% (Table 6.1) and were utilized throughout the year; consequently they must be considered as items of major importance to this antelope. Wattles and blackwood were also principal foods of the bushbuck (ranked 6th and 3rd respectively) and although only blackwood contributed more than 1% of the overall diet, these Acacia species were consumed throughout the year (Table 6.2) and were of greater importance than any of the other commercial trees. Although wattles are more numerous at Weza, both these and blackwoods are abundant in clearfelled areas, young plantations and along river courses. Acacia species are of little economic importance at Weza, and are primarily used as sources of firewood. Regenerating plants are considered as weeds, and although seeds were never detected in the rumens of either bushbuck and duiker, if they are eaten then both antelope may be capable of dispersing these plants (see Jarman 1976). Superficial surveys of the diets of bushbuck by the Natal Parks Board also revealed considerable quantities of wattles in the rumens of these antelope (R. Collinson, pers. comm.; O. Bourquin, pers. comm) and there is no doubt that bushbuck and duiker can cause extensive damage where wattles and blackwood are grown for commercial purposes (De Zwaan 1977; A. Schonen, pers. comm.). Both indigenous and exotic Acacia species are important in the diets of a number of tragelaphids and other ungulates (e.g. Wilson 1965; Littlejohn 1968; Tello and van Gelder 1975; Krausman 1978; Leuthold 1979; Owen-Smith 1979; Owen-Smith et al. 1983).

Green pine needles were the ninth and fifteenth most important annual foods of duiker and bushbuck respectively, but only duiker ate these in sufficient quantities to warrant their inclusion as a principal item of the diet (Tables 6.1 and 6.2). Both bushbuck and duiker ate most green pine needles in winter and early spring (Figs. 6.12 and 6.13). Although Short (1971) found that loblolly pine samples were highest in nutrient quality during spring, the few pine buds or shoots found in rumen samples (recovered from only four duiker and one bushbuck and never exceeding a volume of 1,0

ml) suggest that needles were probably accidentally eaten by both these antelope while feeding on more nutritious foods during spring . Simpson (1974b) claimed that terminal buds and twigs were destroyed by mastication prior to ingestion in the bushbuck rumens he analysed, but he was able to count 360 ripe fruits in the rumen contents from a single animal. Mastication as a reason for the rarity of pine buds and shoots in rumen samples from Weza is considered unlikely because of the high proportions of soft mast and fungi that were eaten intact and were readily identifiable in the rumen contents of both bushbuck and duiker (see Plate 6.1). Since dead pine needles are likely to have even less nutritional value than green needles, their use may be also incidental to the use of more nutritious or preferred plants. A significant correlation was found between the % volume of brown pine needles (which ranked twelfth in the overall diet) and the % volume of fungi consumed by duiker ($r=0,367$; $d.f.=122$; $p<0,001$). Although no such relationship existed between the consumption of brown pine needles (which ranked ninth and were eaten by 112 bushbuck) and fungi (eaten by 8 animals) in the bushbuck samples, dead needles may have been consumed while bushbuck fed on other plants. Odendaal (1983) also suggested that dead pine needles were inadvertently consumed by foraging bushbuck, while the accidental ingestion of non-preferred species has also been noted in other ungulate studies (e.g. Bergerud 1972; Leslie et al. 1984). Rumen analysis of five duiker and six bushbuck collected in winter by Natal Parks Board personnel indicated a higher utilization of pines on private plantations than occurred at Weza. Pines contributed 21% and 29% of the duiker and bushbuck diets respectively, but these analyses were performed using the point-frame method, which is likely to bias the results in favour of pine needles, particularly since larger fragments such as Physalis sp. and Solanum sp. fruits were also consumed by these animals (R. Collinson, pers. comm.; O. Bourquin, pers. comm.).

Young pine compartments are well distributed throughout Weza, and many of the older stands have regenerating pines in the understory. In addition, fresh foliage from pine trash

resulting from pruning, thinning and felling activities (which is readily eaten by cervids in Europe, see Jackson (1977, 1980) and Marcstrom (1977)) is commonly available throughout the plantation. As a consequence of this abundance of pine browse available to bushbuck and duiker, and their light level of utilization, it is highly probable that pines are non-preferred species or foods of minor importance to these antelope. Pines are commonly unimportant in the diets of North American cervids, although they are utilized most during the winter months (Korschgen 1952 cited in Dunkeson 1955; Anderson et al. 1965; Della-Bianca and Johnson 1965; Allen 1968; Nixon et al. 1970; Lawrence and Biswell 1972; Halls 1975; Harlow et al. 1975; Wetzel et al. 1975; Peek et al. 1976; Puglisi et al. 1978; Blair and Brunett 1980; Tilton and Willard 1981; Crawford 1982; Adams and Bailey 1983). The importance of pines as winter foods for deer appears more varied in Europe (Dzieciolowski 1970; Borowski and Kossak 1975; Kossak 1976; Jackson 1977, 1980; Morow 1977; Henry 1978; Hosey 1981; Kaluzinski 1982; Perzanowski et al. 1982) although levels of utilization may be influenced by numerous factors (see 6.4.2) including the availability of different pine species (e.g. Kossak 1976; Mitchell et al. 1977), the availability of alternative foods (Korschgen 1962; Borowski and Kossak 1975; Jenkins and Reusz 1969) and ungulate densities (Nellis and Ross 1969; Blair and Brunett 1980).

Nevertheless, pines and other conifers have been termed starvation foods in both continents (Brandborg 1955 cited in Adams and Bailey 1983; Korschgen 1962; Segelquist and Green 1968; Borowski and Kossak 1975; Kossak 1976) and the avoidance or low levels of utilization of pine species is undoubtedly due to their poor digestibility and quality as a forage. Chemical analyses of all parts of various species of pines, sampled throughout the year, indicate low protein values ranging from 3,8 - 9,6%, fat levels from 4,2 - 31% (but usually under 10% or 4 -5 Kcal/g), and a crude fibre content of approximately 30% (Lay 1957; Ullrey et al. 1967; Short 1971; Gurchinoff and Robinson 1972; Lawrence and Biswell 1972; Oldemeyer 1974; Morow 1977; Blair et al. 1977;

Conroy et al. 1982). The high lignin and crude fibre content of pine suggests that this browse may be retained in the rumen for longer periods than more succulent and digestible foods; consequently the importance of pine as a food for bushbuck and duiker determined in this study may be exaggerated.

While pines are obviously of low nutritional value as sources of protein or energy, their consumption may provide alternative benefits to forest wildlife. Pine browse may be consumed by deer to supplement concentrated diets rich in protein or carbohydrates (Szukiel 1981), to provide trace elements, minerals, vitamins, alkaloids and tannins (McIntyre 1972; Mitchell et al. 1977) or as a source of water (Lockie 1967).

Other timber species of commercial importance at Weza and elsewhere include gums and poplar. The consumption of gums by bushbuck and duiker was confined to the late winter and early spring months, and although gums were more important to bushbuck (Fig. 6.13) and ranked eighth in their diet, it is highly probable that the foliage that was eaten came from regenerating plants which are considered a weed at Weza. Local farmers growing gums on a commercial scale have reported negligible or superficial damage to gum seedlings even when plants are individually fertilized. While utilization studies indicated moderate levels of damage to poplars in winter, rumen samples suggested that both bushbuck and duiker consumed the foliage of this species chiefly in spring and summer (Figs. 6.12 and 6.13), but, as with gums, these were usually eaten at trace levels. Consequently, rumen analyses suggest that antelope browsing plays a minor role in limiting the growth of these timber species.

6.4.1.5 Forage overlap

Because they do not convey information concerning food availability or abundance, similarity indices obtained from

two sympatric herbivore diets indicate only if there is a potential for competition; dietary overlap alone is not sufficient evidence for exploitative competition (Colwell and Futuyuma 1971 and Pianka 1976 both cited in Hanley 1982; Jarman 1971; Anthony and Smith 1977). For example, a high dietary overlap during periods when food is very abundant would not infer interspecific competition. Consequently, although bushbuck and duiker both ate significantly fewer plant species in the spring, it is highly probable that these antelope were selecting a few highly nutritious but abundant species that had recently flushed (e.g. bramble). Simpson (1974b) stated that the high representation of an Acacia species in the food sample together with the large proportion of bushbuck with only a single species in their rumens demonstrated the severity of the environment in which they were culled, which was subjected to extreme hunting pressure. However, it is difficult to envisage the adaptive significance of bushbuck feeding entirely on one species simply as a result of intensive hunting.

Overlap in bushbuck and duiker diets at Weza was greatest in spring and least in winter. With few exceptions these trends were reflected in plant part and forage class use and in each of the principal food items consumed by these antelope (Fig. 6.11). Physiological condition indices and mortality rates (Chapter Four) together with the highly seasonal utilization of plant species available throughout the year indicate that winter is a period of nutritional stress for both bushbuck and duiker. These findings are therefore consistent with the prediction that dietary overlap is lowest during periods of limited forage quality and availability to minimize interspecific competition (Zaret and Rand 1971 cited in Leslie et al. 1984; MacArthur 1972 cited in Dailey et al. 1984; Weins 1977 cited in Hobbs et al. 1983). Many other authors have also noted that diet overlap of sympatric animals declines during times of resource scarcity (Olsen and Hansen 1977 cited in Hansen and Clark 1977; Sinclair 1977; Dunbar 1978; Willms et al. 1980; Hobbs et al. 1983; Dailey et al. 1984). Even at times of resource abundance, bushbuck and duiker diets did not overlap by more

than 40% on a monthly basis (October) or 20% on a seasonal basis (spring); consequently it must be concluded that these antelope have markedly dissimilar diets at Weza.

6.4.1.6 The diets of farmland duiker and bushbuck

The winter foods of duiker shot on neighbouring farms were similar to those of Weza duiker in that exotic species dominated their diet. Maize was eaten in greater quantities than any other foods, but was eaten by only 40% of the duiker examined, and consequently had a %PFI lower than bugweed fruits (Table 6.3) which was also the principal winter food of duiker from Weza (Table 6.1). Maize is an excellent food for wildlife, and although it only has a protein content of approximately 9% (Snider and Asplund 1974; Landers et al. 1979) it is readily digestible and when available, is often a staple food of various species of wildlife during autumn and winter (e.g. Korschgen 1962; Nixon et al. 1970; Robel and Watt 1970; Landers et al. 1979; Kaluzinski 1982). Apart from the inclusion of greater quantities of maize, potatoes and beans in the diet of farm duiker (all included as fruits in Fig. 6.14), these animals showed a remarkable similarity in the species consumed and their relative importance values when compared to duiker from Weza during the winter.

As at Weza, the majority of foods eaten by farm bushbuck was not identified. However, grasses and bugweed fruits were clearly of greater importance to farm bushbuck than to the Weza population. Grasses that were of dietary importance were probably agricultural crops such as oats, rye and lucerne that would contain high levels of protein and minerals (Vangilder et al. 1982). Of the farms surveyed in this study, agricultural grazing was more abundant on farms most distant from Weza, although green grass was also periodically available on areas burnt during the previous autumn and on firebreaks of farms closer to Weza. Plants eaten by farm bushbuck but not recorded in the rumens of animals from Weza included fruits of the Mexican hawthorn,

Japanese radish and beans. Hawthorn fruits were readily eaten by duiker from Weza however, and their absence from bushbuck rumens is probably due to the extremely localised distribution of this plant within the State Forest. Crataegus species are eaten by cervids in the northern hemisphere (Martinka 1968; Coblentz 1970; Nixon et al. 1970; Short 1971; Skinner and Telfer 1974; Puglisi et al. 1978; Jackson 1980; Thill 1984) and are commonly considered as highly or moderately preferred foods (Pearson and Sternitzke 1976; Bobek et al. 1979; Blair and Brunett 1980). Similarly the absence of Japanese radish and beans from the Weza bushbuck diet is undoubtedly due to their scarcity in the study area. Apart from these differences, the plant parts and species composition of farmland and Weza bushbuck diets were very similar (Fig. 6.15, Tables 6.2 and 6.4).

As with timber species, local farmers were generally unconcerned about the slight damage bushbuck and duiker caused to agricultural crops. Interestingly, Kaluzinski (1982) has calculated that 1 628 roe deer (which have feeding habits similar to those of bushbuck and duiker) feeding on 4 200 ha of agricultural land (39 animals/100 ha) and with 89% of the diet consisting of cultivated plants, would reduce the plant biomass during the dormant season by a mere 1%. Several farmers in the Weza district actually welcomed antelope use of agricultural produce as they considered this provided information concerning the presence and relative densities of these species that could not be determined by other means, while other farmers actually planted food plots specifically for the benefit of their wildlife.

6.4.2 The Impact of Bushbuck and Duiker on Forest Plantations

Results from the initial utilization assessments conducted at random in 1980 and 1981 (Table 6.5) indicate that browsing damage to young pines was both infrequent and extremely light. Rumen content analyses and food preference trials corroborate this conclusion. These and later surveys

also demonstrated that browsing rarely resulted in pine mortality; studies elsewhere in South Africa and in North America have similarly shown that browsing seldom affects the survival of pines (Staebler et al. 1954; Roy 1960; Lay 1967; Kuen and Bubenik 1977; Black et al. 1979; Novellie and Bigalke 1981) or other conifers (Crouch 1968). Consequently, any genuine conflict of interests between forest and wildlife management at Weza is likely to involve suppressed tree growth, since this could lead to trees of unequal height within a compartment. Provisional surveys conducted during this study suggest that while damaged trees may be appreciably shorter than intact trees one year after browsing (Table 6.6), such differences are negligible two years later. Thus browsing by bushbuck and/or duiker had no significant impact on either tree density or growth. Similar findings have been reported from other studies of antelope damage to pines; Schutz et al. (1978) found that browsed compartments, although "very scruffy at first" tended to "recover completely and attain an even stocking", while Novellie and Bigalke (1981) concluded that light browsing on seedlings is unlikely to have any effect on the final economic value of the trees. Dunkeson (1955) has also commented on the rapid recovery of browsed pines two years after they were damaged, and Campbell and Evans (1975a) estimated that stems of 35% of the trees in a plantation can be browsed by deer before stands lose significant height.

The effect of browsing would be more serious at Weza if bushbuck and duiker repeatedly damaged individual trees, but this study suggests that seedlings are browsed only during the first winter after planting. Novellie and Bigalke (1981) also found negligible rebrowsing by antelope in their study. Elsewhere in more temperate regions, where pines may be browsed for up to 10 years after planting, repeated damage may lead to a notable suppression of tree growth (Roy 1960; Maxwell 1968; Black et al. 1979).

Later in this study it was evident that the incidence of browsing could be high in localised areas and under certain conditions, and there is no doubt that antelope may cause

substantial damage in certain instances (van den Busche pers. comm.). This study suggests that it is the intensity of the damage, rather than its frequency, which is of concern. However, even if tree growth is suppressed or distorted by browsing, (which has yet to be substantiated in the study area) damage would have to be extremely severe for this to have any financial consequences. This is because the thinning regime employed at Weza reduces pine densities to 45% of the original stock (from 1 350 plants/ha to 600 plants/ha) after eight years of growth. The 750 trees/ha that are felled are either uneconomic and left as trash, or less commonly, sold as pulp wood. It would therefore appear that Forestry's concern regarding the level of damage caused by bushbuck and duiker browsing on pine seedlings, which was one of the main factors prompting this study, has largely been unfounded. It is suggested that reports of damage in the past have been overstated, possibly because pine mortalities may have been incorrectly attributed to browsing. The replacement of pine seedlings is an expensive operation and is only considered at Weza if mortalities within a compartment exceed 10%. This study has shown that such levels of mortality caused by antelope damage are highly improbable, and that other factors such as rodent damage, trampling, poor site preparation etc. may be of major importance when blanking is necessary.

Damage to poplar appeared to be more severe than antelope utilization of pines (Table 6.7) but in terms of the numbers of poplars planted at Weza each year, and the absence of any form of protection to the poplar nursery (less than 1 ha in size), such damage appeared to be of little concern to Forestry staff and was not monitored further in this study.

As at Weza, browsing damage to pines in the northern hemisphere is largely confined to the winter months (e.g. Cadman 1967; Gibson 1967; Maxwell 1967, 1968; Marcstrom 1967; Mutch 1967; Grant 1968; Petyt 1968; Jenkins and Reusz 1969). Several of these authors, together with numerous earlier references, consider that pine damage is in direct response to diminishing alternative food supplies (hence the reference

of pines as starvation foods, see above). For example, Blair and Brunett (1980) considered the consistent browsing on non-preferred and common low-choice species, (including pine), by deer as an indication that the animal population exceeded the carrying capacity of preferred foods. Jenkins and Reusz (1969) found that pine damage dramatically ceased once red deer were provided with supplementary feed, and several biologists have advocated the planting of more preferred plants in order to alleviate pine damage (see Chapter Ten). Although plant availability was not monitored at Weza (and therefore conclusions must by necessity be speculative), all available evidence obtained in this study indicate that pine damage is also inversely related to the abundance of other food resources. Pine compartments were most heavily utilized when they were adjacent to, or surrounded by, mature pines with little understory; in afforested rather than reforested compartments where the vegetation was rank and moribund during the winter, and when the biomass of other plants was drastically reduced by cleaning operations. Conversely, pine utilization was least when compartments were adjacent to or surrounded by thickets or indigenous forests; in clearfelled areas where other seral vegetation was available, and where compartments had been left undisturbed during the winter months. Even the preference plots revealed marked differences in pine utilization. None of the pines at Scylla Bridge were browsed, yet all three species were utilized at Weza where densities of duiker and possibly bushbuck were certainly higher than at the former site. It is therefore suggested that browsing pressure may in fact be predicted prior to winter, and that efforts at potential control could be concentrated in those areas considered most vulnerable (see Chapter Ten). Nevertheless, other variables including ownership, slash treatment, aspect, slope, site quality, soil fertility, elevation, and the size of pine seedlings may all influence the extent of damage (Bergerud and Manuel 1968; Lindsey 1975; Black *et al*. 1979; Miller *et al*. 1982). For example, results from this study suggest that smaller pines are more vulnerable and susceptible to damage (and are more likely to die if browsed) whereas Novellie and Bigalke (1981)

found that antelope in their study area (mainly Cape grysbok, (Raphicerus melanotis), but also some duiker) tended to select taller, more vigorous seedlings. In addition, but undoubtedly related to these other variables, individual pines may exhibit a wide range in nutritive content, and consequently individual seedlings within a compartment may be selected in preference to other adjacent pines (see Gurchinoff and Robinson 1972; Morow 1977).

Individual differences in nutritional quality are perhaps of greater importance when considering food preferences, but these were not examined at Weza. In fact, the preference rankings determined during this study must be regarded as rather crude estimates, since no allowance was made for the differing biomass values of available forage between or within the nine species offered. Nevertheless, results obtained from these plots were in close agreement with those obtained from rumen analyses, with wattles clearly of greater importance than any of the other commercially important species and gums and poplars of greater overall value than pines. Although pines were browsed only at Redlands, their levels of utilization suggest that slash pines were preferred to either patula or loblolly pines. Because compartment pine use was related to many other factors, this implied selection could not be tested further, but several other studies have shown that deer may show distinct preferences for certain pine species, although these clearly depend on what other foods are on offer ({Borowski and Kossak 1975; Kossak 1976; Mitchell et al. 1977). Of the three non-commercial species available, pin oak was clearly the most preferred food at both sites, while liquidambar must be considered as unpalatable to bushbuck and duiker. These findings show close agreement with preferences of North American deer; oak is a highly preferred species (see above) while liquidambar is a non-preferred food (e.g. Blair and Brunett 1980; Thill 1984).

The level of plant utilization was considerably higher at the Redlands plot compared to the site at Scylla Bridge. Because duiker were more numerous at the former site, this

suggests that these antelope may be responsible for much of the damage caused to pines. Rumen analyses, the habitat preferences (Chapter Seven) and the habitats where most pine damage was reported all support this assumption that the duiker is the major culprit. Consequently, and where warranted, control measures should be directed more towards this antelope if they are to be effective (see Chapter Ten).

CHAPTER SEVEN
HABITAT UTILIZATION AND SELECTION

7.1 INTRODUCTION

Ungulates very rarely range at random: more often they select certain areas and reject others. An obvious approach to a functional or causal analysis of these selection patterns is to identify a set of parameters such as the abundance of food, availability of shelter, behaviour of conspecifics etc. and to study the variations in the distribution of the animals in relation to variations in these parameters (Duncan 1983).

The values of many relevant parameters may change quite rapidly in both time and space and therefore ideally should be measured a number of times during the annual cycle, while availability should be mapped on a rather fine scale. As Duncan (1980) points out, the work involved in measuring the quality and quantity of the vegetation types occupied by an ungulate may be so demanding that it can be achieved only in exceptional circumstances.

An alternative approach is to stratify the animals range a priori and to examine the use animals make of the strata in relation to the parameters' average values in each stratum (Duncan 1980). The level of habitat stratification will depend on the precise aims of the research, but obviously, the levels identified must be meaningful to the animals if their behaviour is to be understood. Johnson (1980) identified four hierarchical orders of selection which facilitate habitat stratification. First-order selection relates to the physical or geographical range of a species (see Chapter One). Within that range, second-order selection determines the home range of an individual or stable social group (see Chapter Eight). Third-order selection pertains to the utilization of various habitat components within the home range (this chapter). If foraging areas are identified at this level, then the actual procurement of specific food

items from those available at such sites can be regarded as fourth-order selection (see Chapter Six). These selection orders may of course be divided even more finely. For example, habitats may be categorised according to the amount of protection they afford against predation on either young or adult animals (e.g. Staines 1974; Barrett 1984; Riley and Dood 1984). Furthermore, selection patterns may differ seasonally and may often be more specific during winter months (Nudds 1980; Pierce and Peek 1984), while selection patterns may also differ between the sexes (Peek and Lovaas 1968; Watson and Staines 1978), between animals of differing age (Tilton and Willard 1982) between females of differing reproductive status (Clutton-Brock et al. 1982a) or even between peers (Irwin and Peek 1983; Pierce and Peek 1984). Ideally, because numerous environmental and social factors may influence the use of habitats by mammals, the researcher should take into account the size of the animal under study, its resource requirements for shelter, cover, food and water and its social system (Duncan 1983). However, since there are many interrelationships between the habitat types normally occupied by that animal and its size, general morphology, food habits, social and spatial organisation and antipredator behaviour (see Estes 1974; Jarman 1974; Geist 1974; Leuthold 1977), it may be exceedingly difficult to separate the functional importance of each of these factors. Consequently, habitat utilization and selection patterns are most commonly examined at the population level and are based largely on the utilization and availability of food and cover (see below).

Problems of identifying which factors are responsible for the overall pattern of habitat selection exhibited by a species are further compounded when a population occupies an area that is intensively managed. Such a situation exists at Weza, where the primary management objective is to maintain or indeed enhance timber production. Silvicultural and exploitation practices result in a rapid advancement of successional stages that favour commercially important species and habitats are therefore constantly modified throughout the plantation area at all times of the year.

Until the habitat selection patterns of bushbuck and duiker are identified, and the impact that timber management practices have on these populations is assessed, the management of these antelope will continue to be highly subjective. Once such identifications and assessments have been made, it would then be possible to evaluate other timbered areas for their potential to support these antelope populations (e.g. Stocker and Gilbert 1977). This chapter considers the patterns of habitat utilization and selection exhibited by bushbuck and duiker; the impact of Forestry practices and how these may be manipulated to enhance the quality of wildlife habitats at Weza are discussed in Chapter Ten. As with food preference studies (see Chapter Six), conclusions regarding habitat selection largely depend on the researcher's notion of what habitat components are available to the animal. The numerous methods of obtaining utilization and availability data described in the literature (see below) indicate dissatisfaction with at least some of these, and emphasis in this study was placed on identifying the most suitable and reliable techniques appropriate to the prevailing management conditions at Weza.

7.1.1 Methods currently employed in the determination of habitat utilization and selection.

7.1.1.1 Collection of field data.

Habitat use may be assessed by detecting animal signs such as tracks, bedding sites, evidence of browsing or faecal pellets within quadrats or transects of predetermined size. Alternatively study animals may be monitored directly either by field observations or radio tracking.

Numerous studies have employed animal tracks as a means of utilization assessment, but these have frequently been confined to temperate areas during winter when recently formed tracks are easily detected in snow (e.g. Telfer 1970; Peek et al. 1976; Bloom 1978; Singer 1979; Cairns and Telfer 1980; Morgan and Gates 1983). Tracks may be detected at

other times of the year by preparing or selecting sites in such a way that old tracks are obliterated and new tracks are conspicuous (e.g. Kohn and Mooty 1971; Irwin 1975; Kearney and Gilbert 1976; Brusnyk and Gilbert 1983; Sweeney et al. 1984). A slightly different approach has been adopted by McCaffery (1976) where trails rather than sets of tracks were counted throughout the year. This author found that trails in all forest habitats were formed in proportion to the abundance of deer and not as a function of ground cover characteristics.

Counting tracks or trails may yield some index of usage but these only reflect voluntary movement patterns and do not in themselves indicate how the habitats are used. Bedding sites may be detected in much the same way (Franzmann et al. 1976; Kearney and Gilbert 1976; Tilton and Willard 1982; Pietz and Tester 1983; Monthey 1984), particularly if signs of spoor are followed or backtracked (e.g. Armstrong et al. 1983), while evidence of feeding may be obtained by noting freshly browsed plants along such tracks (Nixon et al. 1970; Kohn and Mooty 1971; Wetzel et al. 1975; McNicol and Gilbert 1980).

These methods are only successful if clearly identifiable signs can be detected, and thus their utility may be confined to certain times of the year. Further problems are likely to be encountered in the interpretation of data, for example, where tracks intermingle (Franzmann et al. 1976) or animals follow a distinct path (Telfer 1970; Singer 1979; Armstrong et al. 1983). There are several other potential limitations regarding interpretation and sampling associated with these methods that apply equally to faecal pellet counts; these are detailed below.

Measuring the distribution of faecal pellet groups has been a popular means of assessing ungulate habitat utilization in both Europe (e.g. Batcheler 1960; Staines 1977; Papageorgiou 1978b; Henry 1981) and North America (e.g. Gill et al. 1975; Ffolliott et al. 1977; Short et al. 1977; Lyon and Jensen 1980; Rose 1982; Kirchhoff et al. 1983; Loft

and Menke 1984). Most commonly, faecal pellet groups are removed from the transect (e.g. Rogers et al. 1958; Beasom et al. 1982b; McCullough 1982; Marcum and Scott 1985) or else marked in some way (e.g. Papageorgiou 1978b; Cairns and Telfer 1980) to avoid repeated counts. In this way plots initially surveyed and then revisited some time later can provide data regarding faecal deposition per unit area per unit time. Quantified in this manner, the numbers or densities of pellet groups found in each habitat type may be used as a direct measure of utilization (e.g. Wallmo 1969; Krefting 1974a; Telfer 1978; Beasom et al. 1982b; Clark and Gilbert 1982). An alternative means of expressing utilization is to convert pellet group number or density estimates into animal-use days (e.g. Short et al. 1977); such an approach can be used to determine population size as well (e.g. Batcheler 1975; Bailey and Putman 1981; Freddy and Bowden 1983a). This latter method requires a knowledge of the rate at which animals produce faecal pellet groups, a subject which has received considerable attention (e.g. Rogers et al. 1958; Smith 1964; Neff 1968). However, either unmodified method assumes that defaecation rates are similar at all times and in all areas; such an assumption may not be valid (see below). Further problems associated with faecal pellet group counts include decisions regarding the selection of plot size and shape and sampling intensity (Neff 1968; Batcheler 1975; Freddy and Bowden 1983a) what constitutes a group of pellets (Strong and Freddy 1979; Welch 1982; Freddy and Bowden 1983a) the age of the faecal pellets, which is particularly important in considering temporary versus permanent (i.e. cleared) plots (Freddy and Bowden 1983b) and determining the rate at which pellets decompose or disappear (Batcheler 1975; Wigley and Johnson 1981). All of these aspects have received attention because there are many potential sources of inaccuracy associated with this technique (Putman 1984) whether it be used for habitat use or population estimation purposes. These may be briefly summarised as:

a) Heterogeneity in the environment. Due to differences in vegetation structure or topography, animals do not utilize

their range randomly. Thus there is a non-random distribution of faecal pellets over the entire area. Stormer et al. (1977) found that frequency distribution of pellet groups could be described by a negative binomial distribution which is defined by two parameters, a positive exponent K and the mean, m. Statistical analyses and interpretation could be greatly facilitated if a common K existed among the pellet distributions for all habitats and for different years. This hypothesis was rejected even for a given habitat examined over 3 years (Stormer et al. 1977). As a result of these distributions, sample variances based on plot counts tend to be large, and acceptable precision can only be generated by increasing the sampling intensity through surveying large numbers of plots (Freddy and Bowden 1983a).

b) Irregular defaecation rates. Defaecation may not be regular throughout the day: animals may defaecate more at certain times of the day (e.g. Welch 1982) or after certain activities e.g. deer defaecated while they were feeding but cattle and sheep dung was commonly found where they had been lying or resting in shaded areas (Julander 1958). Similarly, Henry's (1981) results suggested that defaecation in roe deer was associated with feeding, while Jackson (1974), cited in Henry (1981), observed that fallow deer usually defaecated after rising from their bedding areas. Consequently, defaecation rates may vary in different habitat types (see Collins and Urness 1981; these authors noted that mule deer defaecated only when feeding (70% of defaecations) or travelling (30%) yet travelling accounted for only 4% of the daily activity budget). Furthermore, animals may defaecate at selected sites within their range, particularly in territorial species (e.g. dung piles, see Leuthold 1977; Walther 1978; Boshe 1984). For this reason, care should be taken in considering the removal of dung from one site and placing in in an adjacent (non-surveyed) area. Such a practice may elicit a response of increased localised defaecation in territorial species (Leuthold 1977) either at the original site, or at the dumping site where it will not be detected. Finally, there may be sex and/or age differences in the rate at which faecal pellets are produced

and deposited. Franzmann et al. (197) found significant differences between the daily deposition rates of male and female moose. This would necessitate knowledge of the sex and presumably age structure (see Smith 1964) of the population before the pellet count could be used as a census technique or as a reliable indicator of habitat utilization. Individual variation in defaecation rates have also been noted (Tinnerman (1974) cited in Franzmann et al. (1976) reported that daily deposition rates for moose ranged from 9,6 to 32,2 deposits/day). Factors influencing deposit rate have been reviewed by Neff (1968) and include such aspects as the nutritional value and moisture content of the diet, and captivity.

c) Differential mobility of animals. This may occur at different times of the day of season (see above) or in different habitat types. Consequently, dung will be deposited irregularly in different areas, even though the same daily defaecation rate may be recorded (Putman 1984).

d) Differences in searching ability and interpretation. These may vary according to the personnel employed or as a function of vegetation structure. Neff (1968) claimed that observer bias was the most vexing problem associated with the technique, and although bias was partially a characteristic of the researcher, it was also affected by various aspects of sampling design. The main contribution to observer error was undetected groups of pellets, although differences in interpreting what constitutes a group, particularly when it is scattered, and whether or not it occurs within the sample plot (i.e. if it is on the periphery) were also important aspects. Personal factors such as motivation, fatigue, visual acuity and experience may also be important but are difficult to quantify. In general, observer error will lead to underestimates of pellet group densities, because of the groups that are missed (Neff 1968). Batcheler (1975) ascribed a staggering 5-fold reduction in the apparent number of faecal pellet groups as plot diameter was increased from 71 cm to 700 cm to the difficulties of defining pellet groups, although other workers reviewed in Batcheler (1975)

attributed similar reductions in numbers with increased plot size to the fact that pellet groups were missed. Whatever the cause, these errors were likely to be compounded by searching for pellet groups in habitats with differing ranges of visibility or differing levels of ground cover (e.g. Batcheler 1975; Smith 1978, cited in Freddy and Bowden 1982a; Schmidt 1983). Additional problems may arise in trying to distinguish the age of the pellets in plots that are not cleared, and also in identifying the species that deposited the pellets (these topics were reviewed in Chapter Six).

Attempts to solve interpretational problems, particularly when pellet groups are scattered or intermingled when use is heavy, have included counting the numbers of actual pellets voided at one time. Strong and Freddy (1979) suggested that the number of pellets per group could be used as a criterion for distinguishing old and new groups (reasons for these differences are given below). Their findings were not supported by similar studies of captive (Smith 1964) or wild deer (Welch 1982) where the number of pellets per defaecation for individual animals varied by 100% and from 21-178 pellets respectively. Smith (1964) concluded that pellets voided at one time could be identified by similarities in size, shape and colour while Welch (1982) recommended the measurement of dung volume to overcome these and other limitations.

e) Differential decomposition or disappearance rates of pellets. These may pose serious problems with respect to accuracy of habitat utilization or density estimates, particularly if plots are not surveyed for considerable periods or if temporary (i.e. non-cleared) plots are employed. Pellets may disappear from the original site as a result of climatic influences (e.g. blown away by wind, washed away by rain, buried etc.), trampling, decay or consumption by insects (Neff 1968; Batcheler 1975; Welch 1982). In xeric regions faecal pellets may last for years (Neff 1968; Flinders and Crawford 1977 cited in Wigley and Johnson 1981). However, in more moist areas, entire groups of pellets can disappear within a month, irrespective of

whether these are situated on bare soil or on leaf litter (Wigley and Johnson 1981). These authors suggested that future studies in southeastern United States involving deer pellet groups should be conducted during dry months, but obviously if seasonal trends in habitat utilization are to be determined, periods between initial inspection and counting of pellets should be kept to a minimum where densities of animals are low; such short intervals might necessitate a substantial increase in sampling intensity. Further, since these rapid disappearance rates may be partially due to removal by insects, it follows that greater losses may be experienced in those habitats that favour insect activity.

In conclusion, many of these limitations arise from problems associated with sampling rather than flaws in the actual concept (Putman 1984). Nevertheless most authors, even when using the technique have expressed reservations about its application (e.g. Davis 1977; Rost and Bailey 1979; Loft and Menke 1984). Statements such as "the technique in certain situations provides reliable information" (Kirchhoff et al. 1983) are virtually meaningless if unaccompanied by an commentary regarding what those situations should or might be. Neff (1968) concluded that evaluation of habitat preferences based on pellet group counts should be approached cautiously, largely because the relationship between defaecation and other animal activities remains conjectural. Similarly, Anderson (1969) cited in Collins and Urness (1981) cautioned against inferring the total time ungulates spend in a specific habitat from pellet group counts, because the method assumes a standard daily defaecation rate and that average deposition rate are similar in all habitat types, Despite the fact that the validity of these assumptions has been seriously questioned by detailed studies (e.g. Collins and Urness 1979, cited in Collins and Urness 1981), continued use has been made of this technique, presumably because of its success in reliably estimating ungulate populations in general areas (Collins and Urness 1981).

Possibly because a) the pellet group count technique

does not always reliably estimate deer or antelope preference for various habitat types; b) is expensive to conduct (see Freddy and Bowden 1983b; Schmidt 1983) and c) provides little or no information regarding individual movements, social and spatial organisation and population structure, increasing importance has been attached to more direct methods of habitat utilization assessments, although these too have several limitations.

Direct observations of animals in the field may be conducted in a number of ways. Sightings may for example be based on random or incidental encounters with the subject (e.g. Hall-Martin 1974b; Hanley 1983, 1984), recorded periodically during intensive sampling (Bruns 1977; Irby 1982; Duncan 1983) or obtained from censuses (e.g. Kutilek 1979; Clutton-Brock et al. 1982; McCullough 1982; Penzhorn 1982; Fruzinski et al. 1983). Results are frequently based on sightings of unmarked animals (e.g. Staines 1976; Watson and Staines 1978; Henshaw 1979; Suring and Vohs 1979), although marked animals may provide substantial supplementary data (e.g. Phillips et al. 1973; Zagata and Haugen 1973; Bailey et al. 1983), observations are often confined to daylight hours (e.g. Suring and Vohs 1979; Hanley 1984; Osborne 1984) while extensive surveys can be conducted during aerial reconnaissance (e.g.Phillips et al. 1973; Zagata and Haugen 1973; Pettifer and Stumpf 1981; Rounds 1981; Bailey et al. 1983).

Habitat utilization assessments based on field observations may be influenced by several forms of bias. These include differential visibility within the various habitats being surveyed at any one time as well as at different times of the year, access of roads when observations are made form a vehicle, and biases associated with collar designs of marked animals (Michael 1965; Allen 1968; Martinka 1969; Phillips et al. 1973; Zagata and Haugen 1973; Rounds 1981; Irby 1982; McCullough 1982; Bailey et al. 1983; Hanley 1983, 1984; Sage et al. 1983). Data may also be biased when sightings are made from a vehicle if the study animals show an avoidance of habitats adjacent to roads and

tracks (see Lyon 1979; Rost and Bailey 1979).

Some of these limitations may be overcome either by the use of radio tracking or by methods of data analysis (see below). Radio tracking has become an increasingly popular and important technique in recent years and has been used to determine the habitat utilization of many species of birds and mammals (e.g. Rongstad and Tester 1969; Van Ballenberghe and Peek 1971; Wallestad 1971; Nicholls and Warner 1972; Gilmer et al. 1975; Larson et al. 1978; Wigley et al. 1980; Horkel et al. 1981; Singer et al. 1981; Loft et al. 1984; Schoen and Kirchhoff 1985). Concomitant with this popularity and use has been a substantial increase in the level of sophisticated and automated equipment employed for both data collection and analysis (e.g. see Gilmer et al. 1973; Amlaner and Macdonald 1980). Nevertheless, radio tracking methods are not exempt from several sources of error and bias (Heezen and Tester 1967; Tester 1971; Springer 1979). Accuracy and precision are likely to be affected by a) system errors, which are inherent in the receiving equipment and its operation; b) movement errors, which occur when a moving animal is located by triangulation and two or more bearings are taken at different times and c) topographical errors, which are caused by such factors as reflection and refraction of the signal, resulting in false bearings (Tester 1971; Macdonald and Amlaner 1980). These errors may be substantially reduced by ensuring that simultaneous bearings are taken as close to the subject as possible, and from positions that enable bearings to intersect at approximately 90 degrees (Heezen and Tester 1967; Tester 1971; Springer 1979). Such precautionary measures have been adopted by numerous operators (e.g. Kohn and Mooty 1971; Litvaitis et al. 1980; Hanley 1983; Irwin and Peek 1983; Loft et al. 1984; Pierce and Peek 1984). Errors and biases are obviously less important when radio tracking equipment is being used to locate and make visual contact with the subject (Tester 1971). Indeed, several researchers have deemed it necessary for such an approach for part of their studies at least (e.g. Cumming 1971, 1975; Macdonald 1978; Kenward 1980; Barrett 1984; Jenkins and Starkey 1984; Riley and Dood 1984) although

the value of such a procedure clearly depends on the reaction of the study animal to human presence (see Singer et al. 1981; Young and Ruff 1982). Errors may otherwise be reduced by ensuring that bearings are not taken during period when animals are highly mobile (e.g. Nicholls and Warner 1972; Lindzey and Meslow 1977) or by accepting only those locations that fall within error polygons of a predetermined size or consisting of a single habitat type (Wood and Brenneman 1980; Hanley 1984; Jenkins and Starkey 1984). Singer et al. (1981) did not accept bearings if they formed error polygons, while Pietz and Tester (1983) accepted error polygons in fairly large homogenous habitats but much greater accuracy was required in more discrete and patchy areas. It should however be noted that a minimum of three bearings are required for the formation of an error polygon, and unless three receivers are used simultaneously, errors associated with animal movement are likely; these errors increase as more bearings are taken of the same active animal. Finally potential errors may be reduced by practice, experience and by testing the accuracy using randomly placed transmitters in the field (Macdonald and Amlaner 1980; Witmer and deCalesta 1983; Jenkins and Starkey 1984; Loft et al. 1984; Pierce and Peek 1984).

7.1.1.2 Data analysis and interpretation

Assessments of habitat utilization and selection are subject to the same types of problems, errors and biases associated with the determination of food preferences (see 6.1.1.6). As in dietary studies, the term "preference" does not have a universally accepted meaning (Johnson 1980) and may not be defined or quantified at all (e.g. Joubert 1971, 1973). Even interpretations of the simple measure of habitat utilization may vary. For example, Marcum and Loftsgaarden (1980) state: "Analyses used to determine use of habitat require determining the available area of each habitat category"; it is not known why availability is considered by these authors to be a prerequisite to the evaluation of

utilization. A further similarity between habitat and food preference studies is the wide variety of methods used in their respective analyses.

Determining the proportion of animal signs, sightings and/or locations recorded from radio tracking that occur within each vegetation type is probably the simplest method of expressing habitat utilization. Numerous authors have adopted this approach exclusively (e.g. Allen 1968; Martinka 1968,1969; Bayless 1969; Wallestad 1971; Constan 1972; Wigley et al. 1980; McCullough 1982; Fruzinski et al. 1983) while others have presented such utilization detail but in addition have compared these to the availability of habitats (e.g. Singer et al. 1981; Irwin and Peek 1983; Pietz and Tester 1983; Pierce and Peek 1984).

Methods of physically measuring habitat availability are beyond the scope of this brief review, but decisions regarding what proportions of habitats are available are certainly pertinent. Many researchers have made habitat measurements at random throughout their study areas (Rongstad and Tester 1969; Zagata and Haugen 1973; Collins et al. 1978; Singer 1979; Tilton and Willard 1982; Young and Ruff 1982; Cederlund 1983; Hanley 1983; Irwin and Peek 1983; Pietz and Tester 1983; Witmer and deCalesta 1983; Barrett 1984; Pierce and Peek 1984). Other authors have measured habitat availability only with the area encompassed by the outermost positions of their study animals (e.g. after calculating a composite home range; Kohn and Mooty 1971; Wood and Brenneman 1980; Servheen 1983; Jenkins and Starkey 1984). Yet another means of determining availability is to consider only those areas of vegetation that occur within an individual's home range (e.g. Nicholls and Warner 1972; Gilmer et al. 1975; Hanley 1983, 1984; Irwin and Peek 1983; Loft et al. 1984). Berg and Phillips (1974) adopted a similar strategy but provided mean values of habitat availability in their analyses. This concept of what constitutes available habitat to an individual or group of animals is discussed in detail elsewhere (see 7.4).

Once availability data have been recorded there are a number of methods that can be used to evaluate levels of selection. Suring and Vohs (1979) divided the numbers of observations of deer per hectare in habitat "x" by the percentage of visibility for that habitat. This ratio was used to reduce bias resulting from unequal size of the various habitats, seasonal differences in ranges of visibility within habitats, and differences in ranges of visibility between habitats. In order to eliminate bias from differential habitat availability, Cairns and Tester (1980) devised an affinity index which was the percentage of total pellet group counts on plots in habitat "x" divided by the percentage of study plots in that habitat. Gilmer et al. (1975) adopted a "use index" which was calculated from the number of animals using habitat "x" divided by the number of home ranges containing that habitat. Selection has also been expressed as a percentage of the expected value (determined from the product of the proportion of available habitat by the total number of locations): {(obs-exp)/Exp}x100, with positive and negative departures of observed from expected values (Litvaitis and Shaw 1980). Animal densities have also been used directly or indirectly to evaluate habitat selection (e.g. Jarman 1972; Hirst 1975; Leuthold 1978b, 1978c, 1979; Rounds 1981) where densities are determined from fixed or mean strip widths, or fixed visibility profiles (e.g. Hirst 1969; Norton-Griffiths 1978). The most common means of assessing preference or avoidance however is by examining the ratio of percentage use: percentage availability (or less commonly, the difference between these parameters, e.g. Berg and Phillips 1974; Pietz and Tester 1983). Preference quotients determined in this manner are usually considered to indicate rejection, or avoidance if values are less than 1,0 and indicate selection of preference if values are greater than this; non-selection therefore occurs at values close to unity (Kohn and Mooty 1971; Collins et al. 1978; Horkel et al. 1981; Cederlund 1983; Duncan 1983; Jenkins and Starkey 1984).

Although several authors have presented such data as indicators of habitat selection or rejection (e.g. Cogar et

al. 1977; Collins et al. 1978; Horkel et al. 1981; Loft et al. 1984), these indices alone are not very meaningful without any statistical test of significance. For example, an animal absent from habitat "x" which contributes 1,0% of its home range is not exhibiting the same level of avoidance as say an animal absent from the same habitat where this forms 55% of its range, yet both preference indices would yield a value of 0,0. Furthermore, it is considered injudicious to calculate mean preference indices from several animals (but see Cogar et al. 1977; Odendaal 1977; Horkel et al. 1981), since values indicating avoidance are compressed from 0,0 to some value less than 1,0, while preference values can extend from slightly more than 1,0 to infinity (at least in theory). This constraint has been noted by Duncan (1983) and others and may be partially overcome by normalizing the data using one of several transformations (e.g. Hirst 1975; Duncan 1983; Hanley 1984).

The simplest method of testing whether habitats are used in proportion to their availability is probably chi-square analysis (e.g. Nicholls and Warner 1972; Kearney and Gilbert 1976; Norton-Griffiths 1978; Hanley 1983; Pierce and Peek 1984). If a statistically significant difference is found between the utilization and availability of the habitat types, determination of which vegetation types are preferred can be carried out by using Bonferroni confidence intervals. Such a technique was proposed by Neu et al. (1974) and further clarified by Byers et al. (1984), and has become an increasingly popular method for analysing utilization-availability data (Bloom 1978; Singer 1979; Cairns and Telfer 1980; Servheen 1980; Tilton and Willard 1982; Young and Ruff 1982; Cederlund 1983; Witmer and deCalesta 1983; Jenkins and Starkey 1983; Monthey 1984). However, as Neu et al. (1974) pointed out, conclusions regarding habitat use in relation to availability make two assumptions, namely a) that the animal(s) has an opportunity to select any of the habitat that is deemed available and b) that observations are collected in a random unbiased manner. Clearly, these assumptions are not always met. Penzhorn (1982) ignored 18 of the 38 habitats within his study area

which were either inaccessible or impractical to survey during censuses. Singer et al. (1981) only surveyed high-elevation habitat as a vegetation map was not available for lower areas, while Evans (1979) omitted riverine vegetation as this could not be sampled representatively. Wood and Brenneman (1980) could not detect any level of selection for oak stands (which had been shown to be an important food resource in a companion study) because of the lack of delineation of this habitat from other hardwoods on their vegetation map. The fact that authors have examined habitat availability in their total study areas or in composite or individual home ranges (see above) demonstrates that what is deemed available may differ substantially between researchers and/or for different species. As Marcum and Loftsgaarden (1980) and Byers et al. (1984) point out, records of observations or locations should also be spaced temporally so that the subject has access to the entire area considered. Consequently, when animals have distinct seasonal home ranges, the analysis must be done separately for each season. Failure to adopt such an approach may bias trends in habitat selection, particularly if sample sizes show considerable variation between seasons. Similarly, conclusions regarding preferences may be quite erroneous, despite any accompanying statistical evidence, if key habitats for example are ignored (conclusions in such instances might be that animals showed no selection towards any of the "available" habitats, or that habitat "x" was highly preferred and should be maintained at all costs etc). Consequently, habitat preference ratings should be interpreted with considerable caution for precisely the same reasons as those give in section 6.1.1.6.

In as much as the decision regarding what habitats are available to an animal may be somewhat arbitrary, so too will conclusions obtained from such analyses be arbitrary. In order to eliminate the problems of inexact measurements, Johnson (1980) proposed a novel method based on ranks of components by usage and availability. Habitat use was ranked from the most to the least utilized categories, and habitat availability was treated in a similar manner. Differences

between these ranks provided relative preference values. An advantage of this rank procedure is that it provides comparable results whether a questionable habitat category is included or excluded from consideration, while the relative values discourages any attempts to make absolute statements regarding preference and avoidance (Johnson 1980).

Finally, while conclusions regarding habitat selection may be drawn from these methods (albeit at varying levels of accuracy), they do not necessarily yield information on the functional value of preferred habitats. Such information is best obtained from multivariate statistical techniques (e.g. Ferrar and Walker 1974; Hirst 1975; Melton 1978; Armstrong et al. 1983; Witmer and deCalesta 1983; Loft and Menke 1984) but again, the value of results obtained from these analyses depends largely on a) what the investigator considers available or important to the animals under study, and b) the quality of the original field data (see Melton 1978a; Johnson 1980; Witmer and deCalesta 1983).

7.1.2 Previous studies of bushbuck and duiker habitat utilization and selection

7.1.2.1 Bushbuck

Most general accounts of the habitat requirements or preferences of bushbuck stress the importance of densely structured vegetation to this antelope. Thus, as its name implies, it is usually associated with forests, thickets, wooded areas, bush, scrub and riparian vegetation (Jackson 1955; Dowsett 1966; Mentis 1973b, 1974; Pienaar 1974; Kingdon 1982). This broad acceptance of habitats is undoubtedly reflected in the wide distribution of this species (see Chapter One; Dorst and Dandelot 1970; Pienaar 1974; Evans 1979). Numerous authors have mentioned that bushbuck exhibit a distinct preference for habitats close to permanent water supplies (Stevenson-Hamilton 1947 cited in Jacobsen 1974; Ansell 1960a; Brynard and Pienaar 1960; Pienaar 1963;

Smithers 1966, 1971; Zaloumis and Cross 1974; Jacobsen 1974; Sheppe and Haas 1976; Okiria 1980). Other accounts are more emphatic concerning the dependence of bushbuck on available surface water e.g. "the principle habitat requirements of the species seem to be fairly thick cover and proximity to water so that it can drink daily" (Bainbridge 1973); similar statements that bushbuck are rarely found far from water appear in Shaw (1947); Walker (1975); and Wynne-Jones (1980) and Smithers (1983) while Rautenbach (1982) states "very dependent on the presence of surface water". In contrast, Shortridge (1934) cited in Smithers (1971) recorded bushbuck in "waterless" country, and both Dorst and Dandelot (1970) and Smithers and Tello (1976) have reported that bushbuck are able to exist in areas where surface water is not available for several months of the year.

Ferrar and Walker (1974) found that bushbuck selected woodland and savanna areas in Kyle National Park, Zimbabwe. This preference for wooded, shrubby and patchy vegetation led these authors to conclude that bushbuck could be regarded as having specialised niche dimensions, a narrow niche width and minimal overlap with other ungulates. In contrast, Evans (1979) considered bushbuck as habitat generalists because this species occupied 9 of the 10 habitat categories available in a dry savanna woodland in Malawi.

Four specific studies of bushbuck have quantified levels of habitat utilization selection exhibited by this antelope. Morris (1973) analysed data from 81 culled bushbuck collected during daylight hours in one of four broad habitat categories (river or drainage lines and hilltop or hillside areas, both categories further separated by the presence of cover or reduced cover). The majority of animals (72%) were encountered in river or drainage lines with cover which indicated that cover rather than the water courses themselves were the attractive source for bushbuck (Morris 1973). Reasons why bushbuck were encountered less frequently in areas of higher elevations included the distribution of hunting camps and the greater densities of humans in such regions (Morris 1973).

Waser (1975a) also noted the importance of thickets close to surface water in Rwenzori National Park, Uganda, but these were only utilized during daylight hours; at night bushbuck moved away from the shore and fed in much more open grassland areas,. Waser (1975a) suggested that since bushbuck were rarely observed to drink, proximity to water was not important. Rather, the presence of thickets close to water provided cover for concealment against predators during the day, and he concluded that predation was a primary factor controlling bushbuck activities and spatial distributions.

In contrast, Simpson (1974a, 1974c) suggested that the limiting factor governing seasonal dispersal and concentrations of bushbuck in Botswana was the availability of surface water. Preferences were based on animal densities estimated from censuses conducted along roads in the Chobe National Park. Five habitats were identified and are listed in order of decreasing preference; riparian forest, scrub, thicket, riverine tree savanna and a mixed ecotone complex. Simpson (1974a) maintained that bushbuck were consistently distributed in these five habitats at the same proportions throughout the year, but that overall bushbuck densities in the study area were greatest in the dry season and lowest when surface water was available away from the river during the rainy season.

The results of Odendaal and Bigalke (1979b) are most relevant to this study since they examined day and night habitat selection by bushbuck in a timbered area. Data were recorded from 5 individuals equipped with radio transmitters that were monitored for periods varying from 12 days to 3 months. Gums were generally avoided by bushbuck and these authors suggested that considerable thought be give before planting gums in areas where bushbuck populations are to be conserved. Open areas were also avoided during daylight hours, when habitats providing canopy cover (with or without lateral cover) were most important, but areas devoid of cover were most preferred at night, when bushbuck were presumably feeding. Habitats providing lateral cover only were found to

be totally unattractive. Overall, Odendaal and Bigalke (1979b) found that indigenous forests were the most preferred habitat of bushbuck in the southern Cape.

7.1.2.2 Duiker

Authors generally agree that the duiker inhabits a broad spectrum of vegetation types, provided that sufficient herbaceous or woody cover is locally available. Typical habitats occupied by this species include savanna and woodlands and even quite open areas where there are such patches of cover, which may provide both food and shelter (Smithers 1966, 1971; Mentis 1974; Pienaar 1974; Zaloumis and Cross 1974; Smithers and Tello 1976; Wynne-Jones 1980; Rautenbach 1982). Although this species is the only duiker that is consistently found in open habitats (Dorst and Dandelot 1970; Zaloumis and Cross 1974; Wynne-Jones 1980) it does not utilize forest areas except on the fringes (Dorst and Dandelot 1970; Keymer 1969; Mentis 1973a; Pienaar 1974; Kingdon 1982; Smithers 1983). With the exception of Kingdon (1982), who suggested that competition from other species of duiker and browsing ungulates might be responsible, reasons why forests and other areas of very dense vegetation are avoided have not been offered. Unlike bushbuck, it is generally accepted that duiker are not dependent on permanent sources of open water (Wilson 1966; Wilson and Roth 1967; Evans 1979; Rautenbach 1982).

Two studies have included duiker as part of a general survey on localised herbivore-habitat relationships. Evans (1979) found that duiker utilized 8 of the 10 habitat types studied in Malawi (ranging from open grassland, open woodland and closed woodland with little understory), and concluded that this species by virtue of its broad preferences was a habitat generalist. Ferrar and Walker (1974) also demonstrated a general preference for woodland and savanna areas in this species, but as with bushbuck, considered duiker to be specialists for woody, shrubby habitats.

7.2 METHODS

7.2.1 Vegetation Analyses

Initially compartments within the intensive study areas were examined at bi-monthly intervals. Measurements recorded from the five most dominant species occurring within a randomly placed 5 m quadrat included density, plant height, distribution and phenology. The aspect, distance from permanent water and management history of the compartment was also noted, and other records of the compartment in general included visual assessments of lateral and canopy cover, plant species diversity and a visual appraisal of the homogeneity of the compartment. However, because there were almost 200 compartments in I.S.A.1 alone, maintaining these records proved to be extremely time consuming, and could only be continued at the expense of other aspects of field work, including the monitoring of animal movements and habitat utilization. In addition it was impractical to establish a high number of fixed quadrats, and because of the heterogeneous nature of many of the compartments, consecutive records obtained from randomly placed quadrats within any compartment often showed little agreement. As a consequence of this variability and the time involved in such monitoring, plant measurements were abandoned and habitat classification was based on much broader terms such as the age, density and physiognomy of the dominant tree species, the nature of the understory etc. Assessing trends in animal use of different vegetation types was facilitated by these broader categories, particularly when the data were collected by radio telemetry (see below).

Plant height was however, recorded systematically at 400 m intervals along the 21 km census route in January 1982, at the height of the growing season. The maximum height of the growing vegetation or understory was recorded to the nearest 5 cm (up to a maximum of 250 cm) on both sides of the road and at a perpendicular distance of 5 m, 10 m and 15 m from the roadside. In addition, plant height was also monitored at bi-monthly intervals at 24 randomly placed sites along the

census route. Photographic records were maintained at each of these permanently marked plots in order to assess the impact that forestry management had on the vegetation, particularly the understory. These fixed photographic plots were monitored from January 1981 to April 1982.

7.2.2 Capture and Marking

Emphasis in this aspect of the study was placed on the habitat utilization and selection by known individuals. Since neither bushbuck or duiker could be recognised by means of natural characteristics, animals were marked with conspicuously coloured and coded collars. Animals at Weza were rarely seen during daylight hours however, and even if collared, were also difficult to observe in densely structured vegetation. These problems were obviated by the use of radio tracking equipment, initially kindly constructed by the Department of Electrical Engineering, University of Natal, and later modified by a private concern and subsequently built by the author.

Marking with either visual or radio collars necessitated capture of the subjects and various capture techniques were employed during this study, the most successful being drug immobilization. While the ability to capture and mark a bushbuck and duiker was of vital importance to many aspects of this study, details of such operations are of little relevance to this chapter, and consequently have been detailed in Appendix D.

7.2.3 Field Observations

Prior to capture and marking, all observations of bushbuck and duiker within the extensive study area were made with reference to Forestry's maps (i.e. management block and compartment number). This provided information regarding the types of habitats utilized but, due to highly variable routes of travel, differential ranges of visibility etc. did not

provide any reliable means of determining habitat availability. Details of animals seen within the intensive study area during censuses, capture operations, radio tracking exercises and miscellaneous visits were recorded on gridded maps identical to those used for radio tracking (Appendix D). With experience the vegetation types inhabited by both species of antelope could easily be determined even at night, but localities were still recorded for the purpose of estimating movements and sizes of home ranges (see Chapter Eight). During the last 18 months of field work such details were not recorded from unmarked animals as it was impossible to determine how frequently these animals were observed, nor was it possible to determine what proportion of the study area habitats were available to such individuals. Additional data recorded from all observed marked animals and unmarked animals (up to December 1982) included date and time of observation, group size and composition (including other marked animals), and activity. In addition, every marked animal sighting was sequentially numbered for each specific individual.

7.2.4 Animal Signs

The feasibility of using both tracks and pellet group counts for habitat utilization and population estimation purposes was investigated in 1982. Well-used trails were detected in dense vegetation (e.g. indigenous forests, thickets and riverine areas) but individual spoor could only detected on dirt roads. These were encountered so infrequently (see Chapter Nine) that further attempts to obliterate old tracks and resurvey the area were abandoned. This decision was reinforced by the fact that track counts on roads would have provided very limited data regarding habitat selection, while responses of bushbuck and duiker to roads and roadside vegetation was not known (but see Lyon 1979; Rost and Bailey 1979).

Methods employed for pellet group counts at Weza have been detailed elsewhere (Schmidt 1983). Time constraints, financial costs and the sampling intensity required in a highly diverse study area precluded the continuation of this method for either census or utilization purposes, particularly since other more direct methods simultaneously provided additional data. Other limitations or disadvantages of using pellet group counts at Weza have been listed by Schmidt (1983) and included many of those outlined in section 7.1.1.1. Perhaps the most important of these is that such counts do not yield information regarding the type of use or activity within the prescribed area or habitat (Neff 1968; Davis 1977).

7.2.5 Data Analysis

Habitat utilization was determined from the number of antelope sightings in each habitat type expressed as a percentage of the total number of observations.

All sightings of unmarked animals recorded during culling operations or censuses were used in this analysis, but data from marked animals were confined to those individuals that had been observed and/or radio tracked on a minimum of 10 occasions during any specific season or year. Consequently, total numbers of observations or radio locations exceeded the sum of seasonal records.

Indices of overlap in habitat utilization were calculated in a similar manner to those determined for dietary overlap (Chapter Six); thus the percentage use of each habitat common to both antelope species was tallied on a seasonal and overall basis. Niche widths (W) were calculated for bushbuck and duiker using Leuthold's (1978c) formula of:

$$W = 1/\sum pi^2$$

where pi is the proportion of the i-th resource utilized. For comparative purposes these were then converted to

relative niche widths (Wr):

$$Wr = W/N$$

where N is the number of different habitats utilized. Wr can range in value between 1/N and 1,0 (Leuthold 1978c). In addition, coefficients of species association were calculated on spatial distributions of bushbuck and duiker observed during censuses between September 1980 and November 1981. All sightings were recorded on a 1:12 000 habitat map with a 120 m grid overlay. The formula of Southwood (1965) cited in Western and Grimsdell (1979) was used:

$$1 = 2 \{Ji/(A + B) - 0,5\}$$

where Ji is the number of individuals of species A and B in grids where both are found, A is the total number of individuals of A and B is the total number of individuals of B. This coefficient ranges from -1 (repulsion) to +1 (complete association).

The major habitat types were delineated using Forestry management maps and aerial photographs, both at a scale of 1:12 000 (the latter were taken in colour during June 1983) and by ground reconnaissance. Availability was measured from a revised 1:12 000 vegetation map for each discrete habitat type using a digital planimeter; these areas were then summed for that habitat category and expressed as a percentage of the total area of interest. A composite home range was determined from all bushbuck (or duiker) sightings and radio locations plotted on to this vegetation map by joining up the outermost positions to form a convex polygon (the minimum home range method of Mohr (1947)). Habitat availability for this intensive study area was based on the vegetational state in August 1983 (for further details see 7.3.6.1). Habitat preference indices (H.P.I's) were then calculated as the proportion of bushbuck (or duiker) locations within any one habitat divided by the proportion of the composite home range occupied by that habitat type (i.e. % use: % availability). Levels of significance were deemed necessary for reasons

outlined in 7.1.1.2 and were determined by comparing observed numbers of bushbuck in each habitat type with the expected numbers if all bushbuck had been distributed at random with respect to habitat availability. Chi-square analysis was used for this purpose because the mean density and variance of bushbuck within each vegetation type could not be determined (see Chapter Nine). Since significant results are easily obtained by this method when the sample of locations is large, use was made of the 0,01 rather than the 0,05 level of significance (Norton-Griffiths 1978).

For comparative purposes, use was also made of Bonferroni confidence intervals (e.g. Neu et al. 1974) to determine which vegetation types were preferred or avoided. Because interest was not confined to any one category of vegetation, but rather the entire set of habitat types, simultaneous confidence intervals were constructed using the formula give in Byers et al. (1974). The resulting interval estimates were therefore a 95% "family" of confidence intervals.

Another and more meaningful method of examining habitat preference or avoidance involves investigation at the individual level. Large sample sizes precluded the portrayal of these independently, yet calculating mean H.P.I. values from individual data would be biased. This is because the utilization:availability ratio compresses those habitats that are avoided into a range of 0 to approximately 1,0 while theoretically, preferred habitats have an extended range from 1,0 to infinity. This discrepancy may be reduced by log transformation (e.g. Duncan 1983) but is not eliminated. As a consequence of this constraint, and because both use and availability were undoubtedly measured inexactly (particularly since habitats were being modified by Forestry during field work) the ranking method of Johnson (1980) was also employed. This method obviates the use of absolute statements regarding selection or rejection since ranks, by their nature represent relative values; it is within such a context that the results obtained from this method are discussed.

Johnson's (1980) measure of preference uses the difference between the rank of usage and the rank of availability. In this study the rank of availability was subtracted from the rank of usage, so that positive values indicated a degree of preference. Availability was ranked after the area of each habitat had been measured (by planimeter) within the seasonal or overall home range of the animal being examined. Similarly, distinction was made between usage for each season and throughout the year. Where two or more habitats received equal use or constituted equal proportions to the total area of study, median rank values were used to ensure that the sum of positive ranks cancelled the sum of negative ones for each animal. Individual differences in availability and usage ranks from any one habitat type were then averaged for all animals during the period of interest, and were subsequently compared to determine which habitats were the most preferred and the most avoided. Habitats that were modified during the course of field work (e.g. mature pine altered to a clear felled area) complicated the ranking of availability. However, this problem was overcome by allocating a single category to the area which was based on the longer of the time intervals prior to or after the disturbance or change had occurred. Therefore if a bushbuck was monitored for 17 months and after 12 months a region used by this animal altered from a stand of 3-8 year pines to a stand of 9-13 year pines, then the former vegetation type was allocated to this compartment. Such classifications were therefore made independently of usage. This method was considered preferable to the inclusion of both habitat types, since this would have resulted in an artificial increase in the area used by the bushbuck, although as Johnson (1980) points out, his ranking method is relatively insensitive to the inclusion or exclusion of doubtful components.

7.3. RESULTS

7.3.1. Classification of Habitats

7.3.1.1 Grassland

Grassland occurred on temporary unplanted areas (where discrete patches of bramble were also common) and on cut outs that were periodically burnt during autumn or winter. With the exception of bramble and woody vegetation confined to isolated rocky outcrops, shrubs and trees were virtually absent from this habitat. Common grasses and forbs included members of the following genera: Acalypha, Andropogon, Aristida, Cirsium, Brachiavia, Crassocephalum, Cymbopogon, Digitaria, Eragrostis, Heteropogon, Hyparrhenia, Monocymbium, Panicum, Paspalum, Pentanisia, Plantago, Rhynchelytrum, Rumex, Themeda and Tristachya. Plant height and species composition were influenced by Forestry's burning regime, and by the importance of such sites as grazing areas for domestic livestock.

7.3.1.2 Oaks

All oaks forming a discrete habitat type were mature specimens of Quercus robur. The understory, where evident, consisted of the occasional oak seedling that sprouted during spring and early summer; these were completely utilized by wildlife prior to the succeeding winter. Oak leaf litter and acorns provided the only ground cover during autumn and winter.

7.3.1.3 Cultivated land

Cultivated land included old farmland, derelict as well as maintained gardens, and areas planted for vegetables or fodder crops. With the exception of old farmland and derelict gardens, these sites rarely offered extensive cover but provided a wide variety of food items to bushbuck and

duiker. The most common trees in cultivated land either yielded fruit for domestic consumption (e.g. apple, pear, peach, plum, citrus, mulberry, loquat and fig) or were planted as ornamentals (e.g. oak, elm, hawthorn). Azalea, privet, cotoneaster, and members of the rose family were among the most common shrubs, while the largest areas cultivated for vegetables were planted with maize, potatoes, and cabbages. Ploughed areas provided an abundance of forbs and graminoids in 1982 and were re-ploughed and planted with Eragrostis in 1983.

7.3.1.4 Mexican hawthorns

Mexican hawthorns were confined to a single stand of approximately 1,0 ha in I.S.A.2 which contained nearly 100 mature trees 5-8 m in height. Very little vegetation grew immediately beneath these trees although the ground was covered with fruits during the winter months, and regenerating seedlings, saplings and hawthorns of intermediate age were scattered throughout the stand. Dense thickets of bramble grew in the open areas between the trees, and well worn duiker trails were evident in these thickets which ranged from 0,5 m to over 2,0 m in height. Interspersed with this bramble were various species of grass up to 1,5 m tall, occasional wattles and bugweed while common ground layer plants included Pellaea viridis, Solanum aculeastrum and Duchesnia indica.

7.3.1.5 Indigenous forest

The most common indigenous tree species and the dominant understory vegetation have been listed in Chapter Two (see 2.7.2 and Appendix A.1). Although the species composition of the margins may differ notably from the interior of the forests, no distinction between forests and their ecotones were made in this study as few animals were monitored within this habitat.

7.3.1.6 Riverine areas

Natural riparian vegetation, where this had not been cleared by Forestry, consisted of several species of trees also common in the more mesic indigenous forests, including members of the genera Buddleja, Cassine, Cryptocarya, Grewia, Ilex, Maytenus, Myrica, Rapanea, Rhus, and Trimeria. Several species more commonly associated with water courses were also present, e.g. Alsophila spp., Cliffortia nitidula, Combretum spp., Leucosidea sericea and Rhamnus prinoides. Much of this natural vegetation had been removed in plantation areas, where Acacia dealbata and to a lesser extent Acacia melanoxylon, Pinus patula and Solanum mauritianum were the dominant trees.

7.3.1.7 Thicket

Areas where woody stems exceeded a density of 10 per m were defined as thickets, provided that any canopy present was provided by this density of shrubs and/or trees. Thickets were frequently formed by single species (e.g. regenerating gums or wattles, bugweed or bramble) although mixtures of these together with regenerating pine were also common. With the exception of areas dominated by bramble or bracken, thickets frequently attained heights in excess of 4 metres.

7.3.1.8 Poplar

The majority of poplar areas available to antelope consisted of mature trees, as younger plants were enclosed with electric fencing. Poplars were confined to low-lying areas adjacent to rivers or streams, where bramble, Setaria spp. and bugweed were the dominant elements of the understory.

7.3.1.9 Gums

These have not been planted on a commercial basis at Weza for some time, and all compartments of gums were dominated by mature trees. Regenerating seedlings and saplings occasionally formed a dense understory and midstory respectively but the density of regenerating gums was highly variable. Where sparse, other understory species included regenerating pine, bugweed and bramble. Gum compartments had in the past been designed as fire breaks and often consisted of long narrow belts on high ground. Dense stands of regenerating gums without any overstory component were classified as thickets.

7.3.1.10 Clearfelled areas

Clearfelled areas were one of the most variable habitats at Weza, largely because these sites received considerable attention from Forestry staff for up to three years after felling. Forage and cover availability was directly influenced by the cleaning of these compartments, where the seral vegetation was periodically (once or twice per annum) slashed and stacked. As a result of these activities, reforested areas with pines up to two years of age were included in this category of habitat. Common components of clearfelled vegetation regarded as weeds by Forestry included bugweed, bramble, wattles and numerous other species of shrubs and forbs (e.g. Bidens biternata, Physalis peruviana, Phytolacca heptandra, Senecio spp., Solanum aculeastrum, Tagetes minuta etc.). This vegetation invariably formed a dense ground cover and shrubs and small trees frequently exceeded a height of 2,0 m in the older compartments.

7.3.1.11 3-8 year pines

All compartments with pines older than 2 years but maintained at their original planting density of 1 350 trees/ha were included in this habitat. Patches of bugweed

(up to 5 stems/m^2) bracken and bramble (up to 30 stems/m^2) were common, particularly in the younger or intermediate aged compartments. The pines were clearly the dominant species by the time they were pruned and in all older pine compartments. Pruning of all lateral branches to a height of 3 m occurred when the trees were 6 m tall (usually 6-7 years old) and once the vegetation surrounding the trees had been cleared. The mean height (± S.D.) of the oldest pines in this habitat was 8,65 m (± 0,94 m) when they had a mean diameter at breast height (D.B.H.) of 12,17 cm ± 0,45 cm.

7.3.1.12 9-13 year pines

Pines at a density of 650 trees/ha (i.e. after their first thinning but prior to a second reduction in density) characterised this habitat. Canopy cover thus progressed with age in these compartments. In addition to clearance during thinning, the understory vegetation was frequently removed during second and third prunings (pruning details are presented in Table 2.6). These slashed weeds, together with trash from thinning and pruning, were frequently piled into 1 -1,5 m high parallel stacks. The mean height and D.B.H. of the oldest pines in this habitat were 14,90 m (± 2,15 m) and 18,75 cm (± 1,59 cm) respectively. The dominant species in the disturbed understory were similar to those in 3-8 year pines.

7.3.1.13 14-18 year pines

This habitat was dominated by pines at a density of 400 trees/ha (i.e. subsequent to second but prior to third thinnings), and as with 9-13 year pines, canopy closure proceeded with age. The understory, usually sparser than in the younger pine habitats, was however less disturbed and cleared only during the process of second thinning. The ubiquitous bramble and bugweed were again dominant understory species, while Senecio spp., Pellaea viridis and forest grasses (e.g. Setaria spp.) were also common. The mean

height and D.B.H. of the oldest pines in this habitat were 20,54 m (± 1,42 m) and 23,92 cm (± 1,18 cm) respectively.

7.3.1.14 19-30 year pines

Commercial trees in this habitat were reduced to a density of 250 pines/ha after the third thinning. Canopy closure was completed in the more mature compartments prior to clearfelling. Consequently the understory was often sparse, with species similar to 14-18 year pines but also occasionally including some pine and gum regeneration and fungi. However, at some sites there was a complete absence of an understory, with ground cover limited to dead pine needles.

7.3.2. Vegetation Analyses

An inverse relationship existed between ground cover or understory plant height and successional stage in pine plantations, with clearfelled areas and mature pines (where canopies were invariably closed) exhibiting the tallest and shortest vegetation respectively (Table 7.1). Differences in understory height were significant only between 9-13 year pines and 14-18 year pines ($t=2,71$; $p<0,01$) and between 14-18 year pines and 19-30 year pines ($t=4,49$; $p<0,001$), possibly because these older compartments were less modified by recent timber management practices than younger trees. With the exception of oaks, which lacked any understory, vegetation in all the other habitats monitored was taller than that in 19-30 year pines. Vegetation in the young and intermediate age classes of pine, as well as in poplars and camphor compartments, progressed in height with perpendicular distances from the roadside while understory vegetation in mature (19-30 year) pines, showed the reverse trend. Riverine and grassland vegetation measured at a distance of 10 m from the road was taller than that 5 m or 15 m from the verge, although plant height differences were less between the 10 m and 15 m sites than between the 10 m and 5 m plots.

TABLE 7.1 Mean height of ground cover or understory vegetation in various habitats as determined from 312 measured sites along the fixed census route during the peak of the growing season, January 1982.

Habitat type	n	$\bar{x}$ ht. (cm)	S.E.
Clearfelled	18	121,11	9,20
3 - 8 year pines	27	114,26	8,79
9 - 13 year pines	57	106,93	5,30
14 - 18 year pines	36	82,20	7,85
19 - 30 year pines	54	40,37	5,53
Poplar	12	52,08	9,34
Riverine	21	94,52	9,37
Thicket	9	>250,00	-
Grassland	69	75,65	5,24
Oaks	6	0,00	0,00
Camphor	3	135,00	24,66

7.3.2.1 Forestry's impact on the vegetation

Thirteen of the 24 compartments where fixed photographic points were established were not subjected to any of Forestry's influences. The height of the ground over or understory vegetation at all of these sites was at least as tall in January 1982 as in January 1981, although by April 1982 the effective height in two of these compartments had been reduced by leaf abscission. Similarly, four other compartments had reduced understory during winter due to the death of annual plants, the effects of frost etc.

Three compartments were intentionally burnt by Forestry. This activity was confined to June and July . Only one site had vegetation taller in January 1982 compared to the previous year, but the height of the vegetation in the other two areas was greater in April 1982 than in April 1981 prior to burning.

Cleaning activities conducted independently or in association with thinning or pruning, were carried out in seven of the 24 compartments that were monitored from January 1981 to April 1982. Because these were not confined to any specific time of the year, the precise effects of such operations on the vegetation could not be easily identified or summarised. However, where cleaning had occurred a minimum of six months before this photographic survey was completed (i.e. prior to November 1981) the height of the vegetation in the five cleaned compartments was always greater than that prior to slashing. Plant regrowth was even more rapid in cleaned clearfelled areas, with vegetation height equalling or exceeding the original values within three months of cleaning and often exceeding 50 cm within three months of summer cleaning.

Only one of the 24 compartments monitored in this study was clearfelled in April 1981. The height of the understory prior to felling was 20 cm. Pioneer species did not emerge for six months until the onset of the spring rains, and had attained a height of 50 cm by January 1982; when the compartment was cleaned. Regrowth of this early seral vegetation, together with new invasive species had reached a height of 60 cm in April 1982 when the survey was terminated.

7.3.3 Radio Tracking and Resighting Data

Habitat utilization and selection data were recorded from 74 individual bushbuck (40 males, 34 females) and 38 duiker (21 males, 17 females) that had been captured either in nets or by drug immobilization on a total of 139 and 43 occasions respectively. Of the 74 individual bushbuck caught, 77% were fitted with radio collars, and if recaptured (each animal was caught an average of 1,9 times) this was invariably done to fit or replace radio collars (109 transmitters were placed on a total of 57 bushbuck; 14 animals each received at least three different transmitters during the course of this study while one animal was fitted with a total of seven radio collars). Bushbuck were

monitored by radio tracking for a total of 28,3 bushbuck years and observed for a period of 66,8 bushbuck years (30 individuals were each monitored for periods exceeding one year). Of the 3 415 recorded positions of bushbuck, 48,9% were obtained from radio telemetry and 51,1% from direct observations in the field. The number of daytime (6.00h to 17.59h) locations slightly exceeded those obtained at night (1764 and 1651 respectively). Similarly, data obtained from female approximated those recorded from male bushbuck (Table 7.2).

TABLE 7.2 A summary of locational data from male and female bushbuck.

	Males	Females	Total
No. of observed locations	864	882	1 746
No. of radio locations	807	862	1 669
Total no. of locations	1 671	1 744	3 415

Attempts to fit radio collars to duiker met with limited success, and recaptured animals (each individual was caught on average of 1,1 times) never had their radio transmitters replaced due to the problems detailed in Appendix D. As a consequence of this, together with the fact that marked duiker were resighted much less frequently than bushbuck, data from this species were fragmentary and did not permit seasonal comparisons in habitat utilization or selection. Capture exercises for this species were abandoned at the end of 1982, at which time 8 transmitters had been fitted and had provided a total monitoring time of 1,3 duiker years. Fifteen of the 38 marked duiker were observed for periods of one year or more, and the 461 locations of marked duiker observed in the field were recorded over a period of 45,2 duiker years.

7.3.4 Nocturnal Habitat Utilization as Determined from Culling and Census Data.

Culling operations and censuses were conducted for 47 months and 14 months respectively and during these periods habitats were continually being modified or altered by Forestry staff. In addition, culling operations extended over the entire plantation area. Consequently, it was impractical to attempt any assessment of habitat availability and the data recorded during these operations are simply presented as the proportions of animals observed in the various habitats.

The majority of bushbuck randomly culled at Weza were collected in clearfelled areas followed by grassland and 3-8 year pine (see previous chapter, Fig. 6.1). Seasonally, more bushbuck were shot in clearfelled areas during autumn, winter and spring, while grassland yielded the most animals in the summer and was also an important habitat in spring. Young 3-8 year pines were largely utilized by bushbuck during spring, summer and autumn but were less frequently inhabited during the winter.

Duiker were most commonly culled in grassland and clearfelled areas and in mature (19-30 year) pine stands (Fig. 6.1). Culling success was greatest in grassland during spring and summer, while clearfelled areas and mature pines yielded the greatest numbers of duiker in autumn and winter respectively.

Overall, overlap in habitat utilization was estimated at 69,7% and seasonally was greatest in summer (74,5%) and least in spring (52,8%). Relative niche widths determined from culled animal data were 0,647 and 0,489 for bushbuck and duiker respectively.

Of the 503 bushbuck counted during censuses, 24,1% were each observed in oak and cultivated areas, 9,7% in 3-8 year pines and 8,0% in grassland (Fig. 7.1). The least utilized habitats included gums (0,4%), 19-30 year pines (1,6%) and

9-13 year pines (1,9%). However, disproportionate numbers of bushbuck were counted each season, and these results are heavily biased in favour of winter, and to a lesser extent, autumn sightings. Extensive oak stands and cultivated land (both of which occurred in intensive study areas where no culling took place) were most utilized in autumn (29,4% and 24,4% respectively) and in winter (27,5% and 29,0% respectively). Other important habitats included grass in autumn (10,6%) and 3-8 year pines in winter (9,8%). Habitats not or seldom frequented by bushbuck during autumn nights included gums (0%) and thickets, 9-13 year pines, and 19-30 year pines (all 1,3%). Similarly bushbuck were never observed in gums during winter and were rarely seen in 9-13

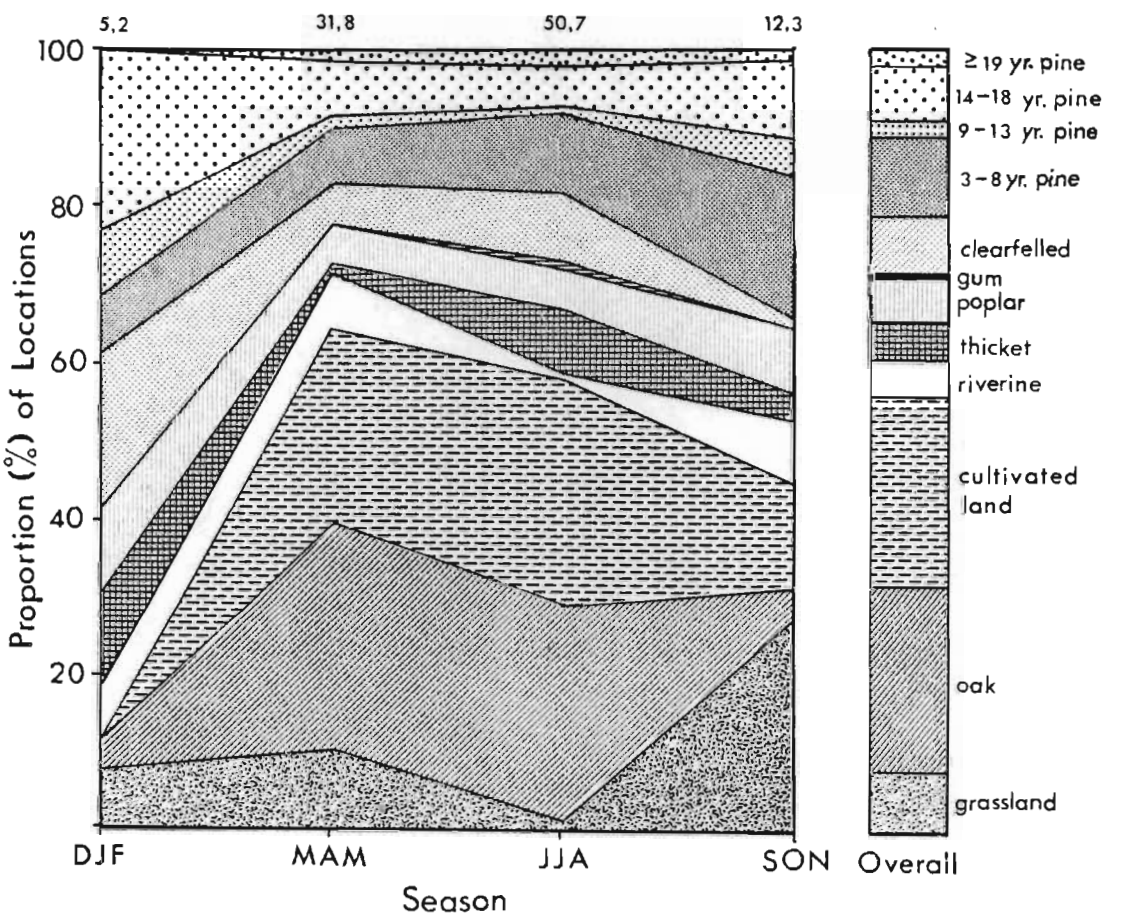


FIGURE 7.1 Seasonal variations in the proportions of bushbuck observed at night in the various habitat types at Weza during censuses. (Values at the top of the figure indicate the percentage of animals observed during that season, total number of observations = 503).

year pines and riparian or grassland areas (Fig. 7.1). Oaks declined in importance in spring when most bushbuck were counted in grassland (27,4%), 3-8 year pines (17,7%) and cultivated lands (12,9%). Again, no bushbuck were observed in gums at this time, and few sightings were recorded from clearfelled sites and mature pines (both 1,6%). In summer, habitat utilization patterns were distinct from those during the rest of the year, and the majority of animals occurred in 14-18 year pines (23,1%), clearfelled areas (19,2%) and in thickets and poplars both (11,5%). Bushbuck apparently remained absent from gums and also did not frequent mature pines and cultivated land while use of oaks was minimal (3,8%) during this time (Fig. 7.1).

A total of 400 duiker were observed during counts, and of these 56,5% were seen in grassland, 10,3% in cultivated areas and 9,8% in 19-30 year pines. Duiker used fewer habitat types than bushbuck and were never observed in riverine vegetation, thickets or indigenous forest while a mere 0,5% were recorded in oaks and 0,8% in poplars. As with bushbuck, duiker sightings were not evenly distributed throughout the year and the proportions cited above were undoubtedly weighted by the high number of duiker (219) seen in winter (Fig. 7.2). Nevertheless duiker were found predominantly in grassland throughout the four seasons (minimum of 52,7% seen in spring and maximum of 63,8% in autumn, see Fig. 7.2). During autumn 14-18 year pines (8,7%) and clearfelled areas together with 9-13 year pines (both 7,2%) were also important habitats, while duiker were not detected in oak, poplar and gum compartments (in addition to the three habitats listed above, where they absent throughout the year). Cultivated land received greater use in winter (15,5%) and 14-18 year and mature pines were also important (both received 8,7% of total winter use) but poplars (0,5%) and oaks (0,9%) continued to be utilized lightly. Older pines (14-18 year and 19-30 year) remained important areas in spring (10,9% and 18,2% respectively) when duiker were again absent from oaks and also clearfelled sites. After grassland areas, duiker were most frequently observed during the summer in areas dominated by the two oldest classes of pines (12,2%)

and in clearfelled areas (8,8%, see Fig. 7.2). Oaks, gums, poplars and cultivated lands were not utilized during this period.

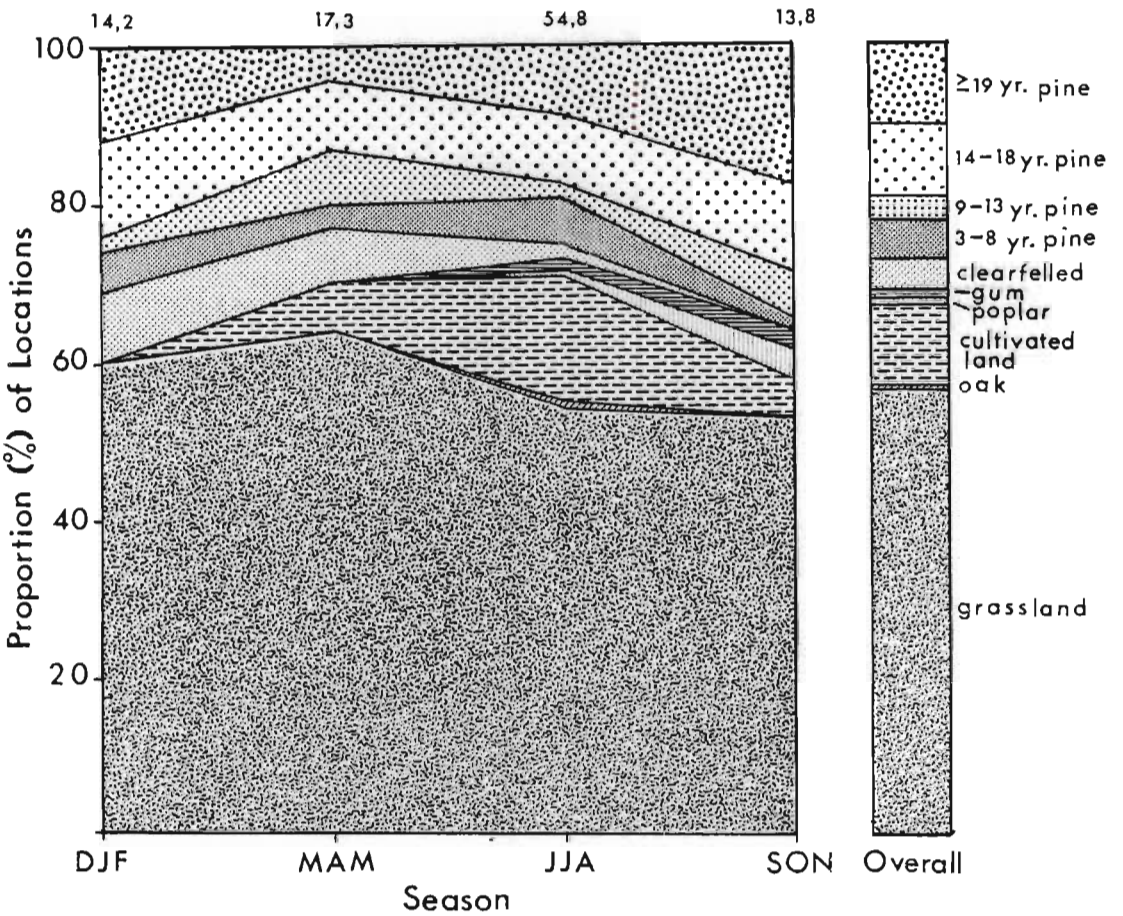


FIGURE 7.2 Seasonal variations in the proportions of duiker observed at night in the various habitat types at Weza during censuses. (Values at the top of the figure indicate the percentage of animals observed during that season, total number of observations = 400).

Considering all seasons, habitat utilization of counted bushbuck and duiker overlapped by 40,0%, substantially less than that estimated from culled animal data. Further differences were evident when the vegetation types inhabited by these two species were examined on a seasonal basis; overlap in habitat utilization was greatest in spring (54,4%) and least similar in autumn (35,0%). As with culled animal data, utilization estimates determined from censuses yielded a large relative niche width for bushbuck (0,551) than for

duiker (0,236).

Even when habitats were shared by bushbuck and duiker, coefficients of species association suggested that bushbuck and duiker rarely intermingled in the same vicinity. Greatest avoidance occurred in Spring (-0,609) and summer (-0,455) and was least in winter (+0,236). Avoidance was consistently more pronounced in the study area favoured by bushbuck (I.S.A.1); both species were more commonly encountered feeding in cultivated lands, which were confined to I.S.A.2, particularly in late autumn, winter and early spring.

7.3.5. Habitat Utilization as Determined from Marked Individuals

7.3.5.1 Bushbuck

For comparative purposes, data from marked individuals (visual as well as radio collared) were analysed in an identical manner to those from bushbuck encountered during censuses. Marked bushbuck locations were however concentrated within I.S.A.1 and included substantial information concerning habitat utilization during daylight hours.

A total of 3 415 marked bushbuck locations were recorded, and 98,5% of these were from animals that were seen and/or located on at least ten occasions. Overall, bushbuck made greatest use of thicketed areas (22,3%) while oaks and 14-18 year pines were also of considerable importance (15,8% and 14,4% respectively, see Fig. 7.3). Habitats receiving little use by bushbuck included indigenous forest (0,3%) poplars (1,3%) and gums (2,7%). Seasonally, bushbuck used thickets extensively throughout the year (from 15,0% in winter to 28,7% in spring, see Fig. 7.3), but oaks were of value only during autumn (21,6%) and winter (28,4%). Bushbuck were also frequently recorded in 14-18 year pines during spring (14,8%), summer (16,8%) and winter (14,8%) while riverine areas had higher percentages of use in summer

(13,6%) and autumn (13,1%) than at other times of the year. Poplars, gums and indigenous forests consistently received little use by bushbuck throughout the year (Fig. 7.3) while grassland areas were least frequented in autumn and clearfelled sites were also of minor importance in winter. Overall, bushbuck had a relative niche width of 0,618 while seasonal values progressed from 0,540 in winter, 0,553 in spring, peaked to 0,623 in summer and declined to 0,570 in autumn.

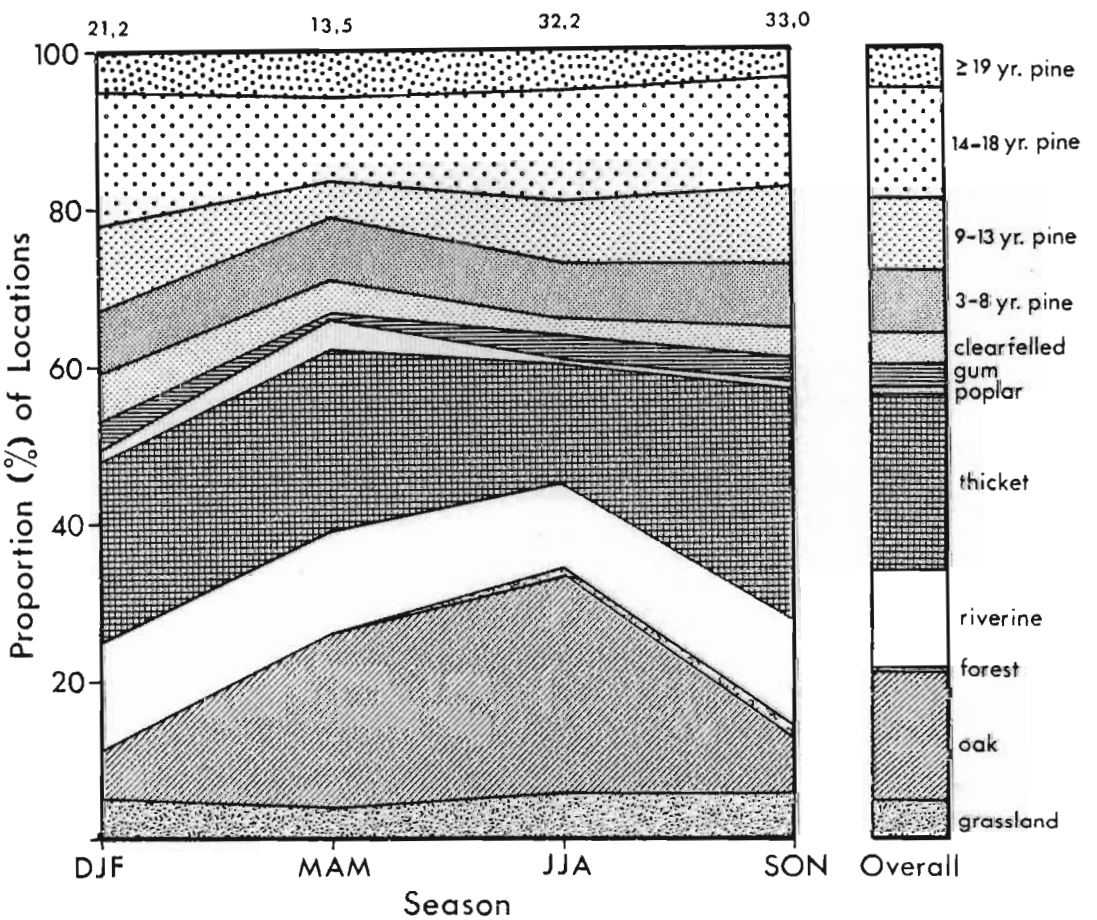


FIGURE 7.3 Seasonal variations in the proportions of marked bushbuck observed and monitored by radio tracking in the various habitat types in I.S.A.1. (Values at the top of the figure indicate the percentage of locations during that season, total number of locations = 3363).

Obvious differences between day and night habitat utilization were evident during the course of this study and all data from monitored animals were subsequently analysed on

a temporal basis. In addition, indices of habitat utilization overlap revealed differences between males and females (overall overlap of 71,1%; overlap of diurnal habitats = 67,3%; similarity of nocturnal habitats = 79,6%). Males also had a greater niche width (0,697) than females (0,547). Consequently, diurnal and nocturnal use of habitats by male and female bushbuck were considered independently.

7.3.5.1.1 Male bushbuck

7.3.5.1.1.a Diurnal use of habitats

A total of 811 locations were recorded from marked bushbuck that had been individually monitored on at least ten separate occasions. These animals spent the majority of their time in thickets (72,0%) and in 9-13 year (15,6%) and 14-18 year (14,1%) pine stands (Fig. 7.4). Use of thickets was particularly pronounced in autumn (45,6%) but declined to 10,4% in summer, while less use of 14-18 year pines occurred in autumn. Other habitats which assumed importance for at least one season included riverine areas (winter = 12,6%) 3-8 year pines (summer = 13,9%; autumn = 6,3%) and mature pines (autumn = 16,4%). Indigenous forests (1,0%) poplars (1,6%) and gums (3,1%) were rarely used by bushbuck throughout the year; clearfelled areas were also of little importance during autumn and winter days, oaks received little use during summer or winter and grassland was least utilized in autumn (Fig. 7.4). Diurnal habitat utilization by male bushbuck indicated a relative niche width of 0,653.

7.3.5.1.1.b Nocturnal use of habitats

Although the 825 locations of marked bushbuck monitored at night indicated that thickets and 9-13 year pines remained important habitats (11,5% and 12,5% of total habitat use respectively see Fig. 7.5), oaks received the most use by males (36,0%) particularly in autumn (39,4%) and winter (52,7%). In addition, bushbuck males displayed a more

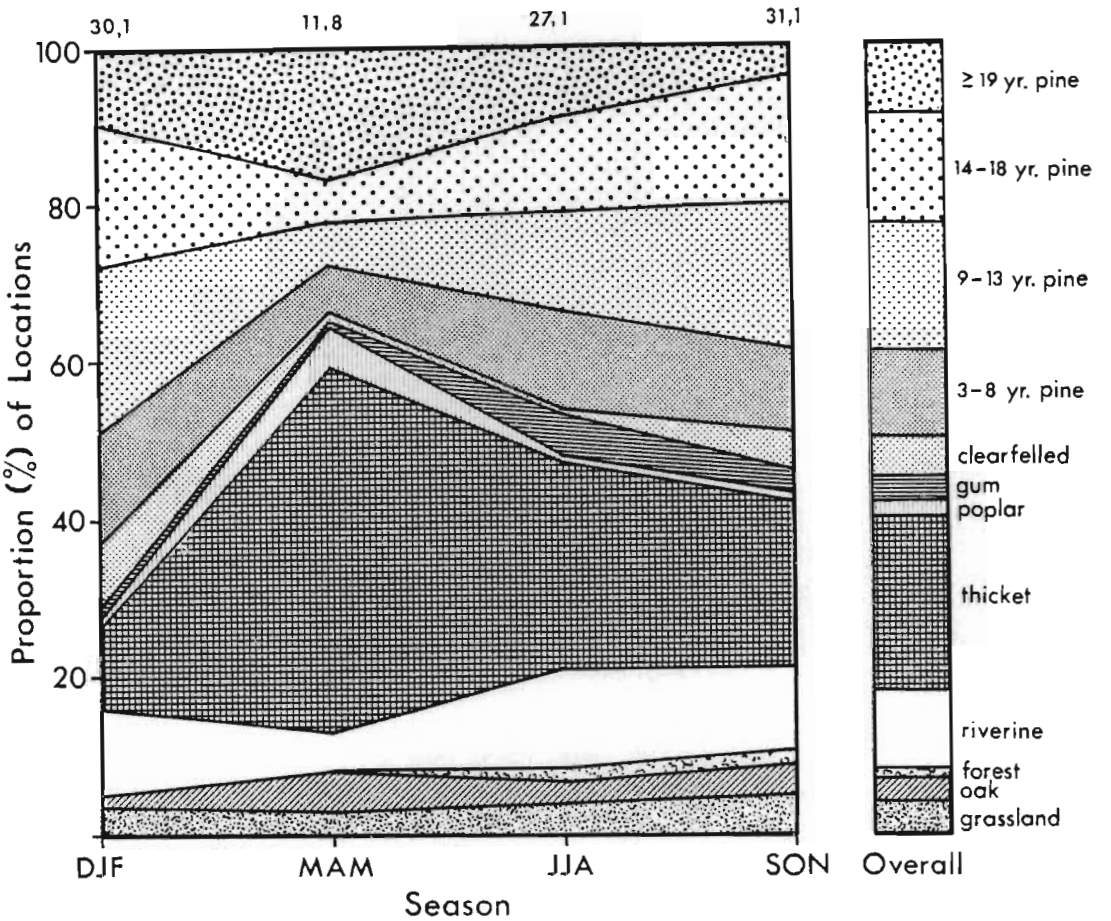


FIGURE 7.4 Seasonal variations in the diurnal habitat utilization of marked male bushbuck at Weza. (Values at the top of the figure indicate the percentage of males monitored during that season, total number of locations = 811).

seasonally diverse pattern of habitat utilization, and in contrast to diurnal use, 14-18 year pines were inhabited infrequently at night. Other habitats of seasonal importance included grassland during the summer (15,7%), 3-8 year pines and poplars in autumn (12,8% and 11,7% respectively) when 9-13 year pines were not utilized, and clearfelled areas in the spring (10,5%, see Fig. 7.5). Overall, as during daytime monitoring, few males were recorded in indigenous forest, gums and poplars (0,3%; 1,65% and 2,8% respectively) and 19-30 year pines were rarely inhabited in spring, summer and autumn. During autumn bushbuck were absent from grassland and 9-13 year pine areas, and 3-8 year pines and 14-18 year

pines were least utilized in winter and summer respectively (Fig. 7.5). The relative niche width of male bushbuck habitat utilization at night (0,525) was less than that for daytime use.

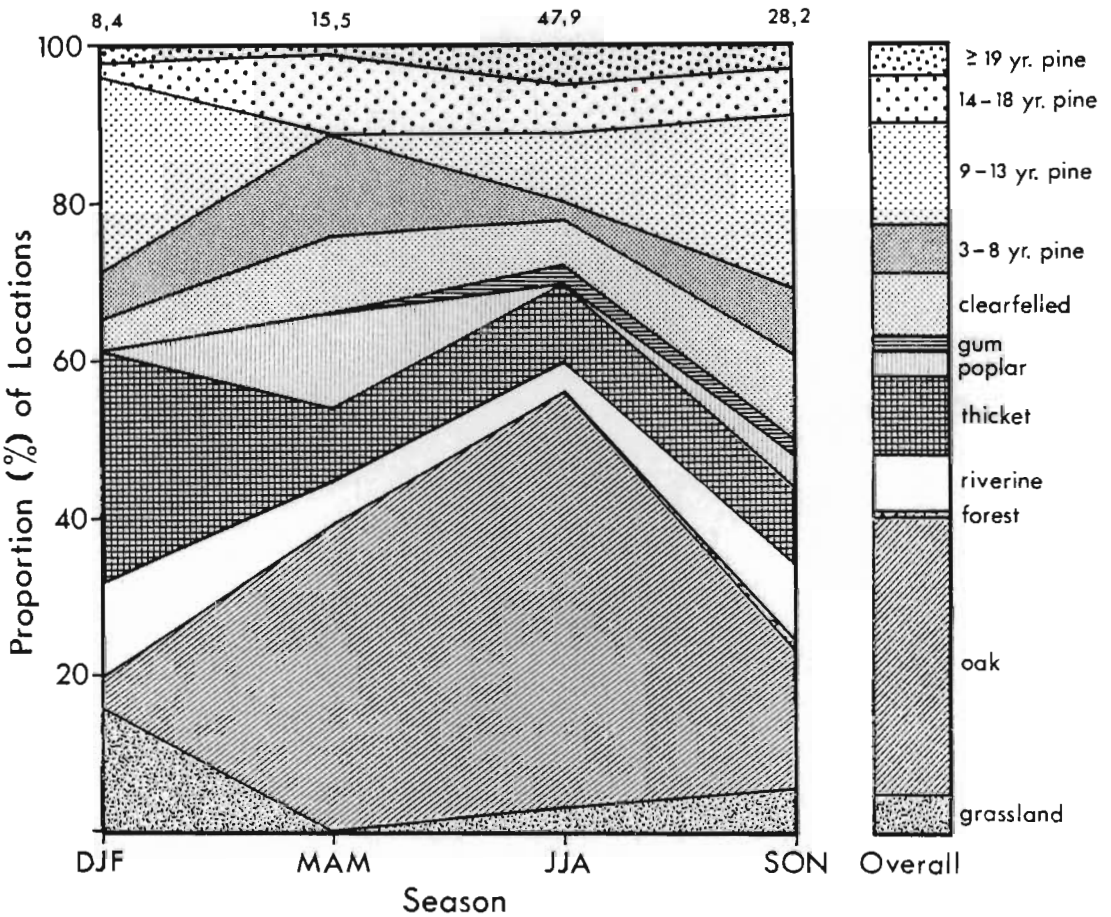


FIGURE 7.5 Seasonal variations in the nocturnal habitat utilization of marked male bushbuck at Weza. (Values at the top of the figure indicate the percentage of males monitored during that season, total number of locations = 825).

7.3.5.1.2 Female bushbuck

7.3.5.1.2.a Diurnal use of habitats

Diurnal habitat utilization patterns based on 869 locations of individual marked females each located at least 10 times resembled those of males in that thickets and 14-18

year pines were frequently used (28,1% and 19,6% respectively) but riverine areas were much more important (15,1%) than 9-13 year pines (5,3%) for females. With the exception of autumn, when use of 3-8 year pines exceeded that of 14-18 year pines, these three habitats remained the most heavily utilized throughout the four seasons (Fig. 7.6). Female bushbuck were never encountered in indigenous forests during the day, and only rarely used poplars (1,7%) and clearfelled areas (2,2%) except in autumn (when gums were infrequently inhabited) and summer respectively (Fig. 7.6). As with males, grassland and oaks were consistently used at low levels throughout the year. The relative niche width for females at this time was 0,518 which was lower than the corresponding value for males.

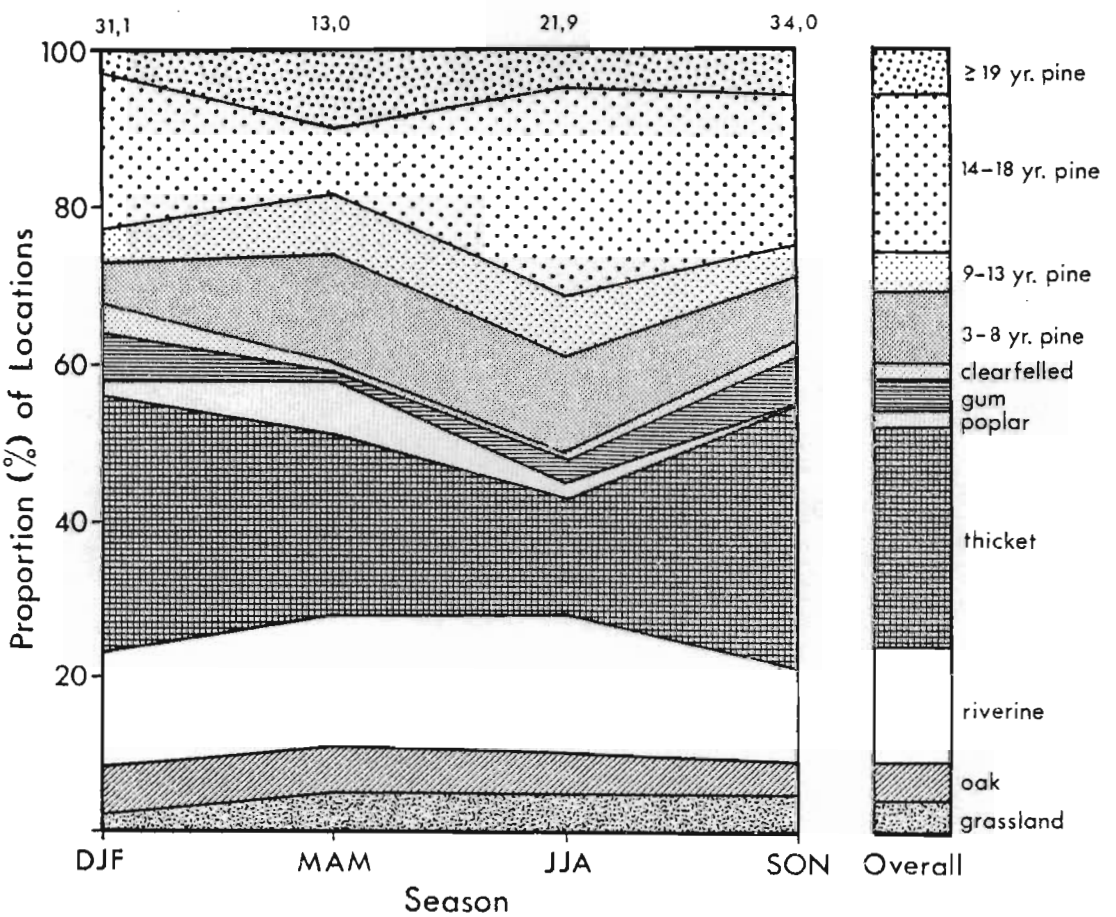


FIGURE 7.6 Seasonal variations in the diurnal habitat utilization of marked female bushbuck at Weza. (Values at the top of the figure indicate the percentage of males monitored during that season, total number of locations = 869).

7.3.5.1.2.b Nocturnal use of habitats

A total of 858 nocturnal locations indicated that females displayed a similar prevalence for oaks (24,5%) and thickets (21,0%) but unlike males, 9-13 year pines were of little or no importance and instead riverine areas and 14-18 year pines received much greater levels of utilization (17,1% and 15,4% respectively, see Fig. 7.7). On a seasonal basis, female bushbuck utilized oaks predominantly in autumn (43,4%) and winter (38,1%) and thickets were most frequently inhabited in winter (12,5%) spring (36,9%) and summer (13,7%). Riverine areas were occupied most in spring, summer and autumn while 14-18 year pines were consistently one of the three most utilized areas throughout the year (Fig. 7.7). Habitats never or rarely used by marked female bushbuck included indigenous forest, clearfelled areas and mature pines. Female bushbuck use of poplars was confined to the spring months, and although gums received greatest proportional use in summer, this vegetation type, together with 9-13 year pines, never accounted for more than 5% of the total habitat usage in any season. As with male bushbuck, females had a lower relative niche width at night (0,485) than during the day; this value was also lower than the corresponding value for males.

7.3.5.2 Duiker

Despite repeated efforts to obtain resighting records of duiker in the field, relatively few animals were observed throughout the year. Transmitter malfunctions (e.g. inadequate power supply, short circuits etc.) compounded the problem. Consequently, far fewer locations were recorded for duiker than for bushbuck (recorded positions from individuals monitored on at least 10 occasions totalled 425, while even fewer records were available from animals seen and/or radio tracked for a minimum of 10 times during any one season, see Fig.7.8). Due to this paucity of data it was not feasible to consider the sexes separately or to distinguish between diurnal and nocturnal use of habitats.

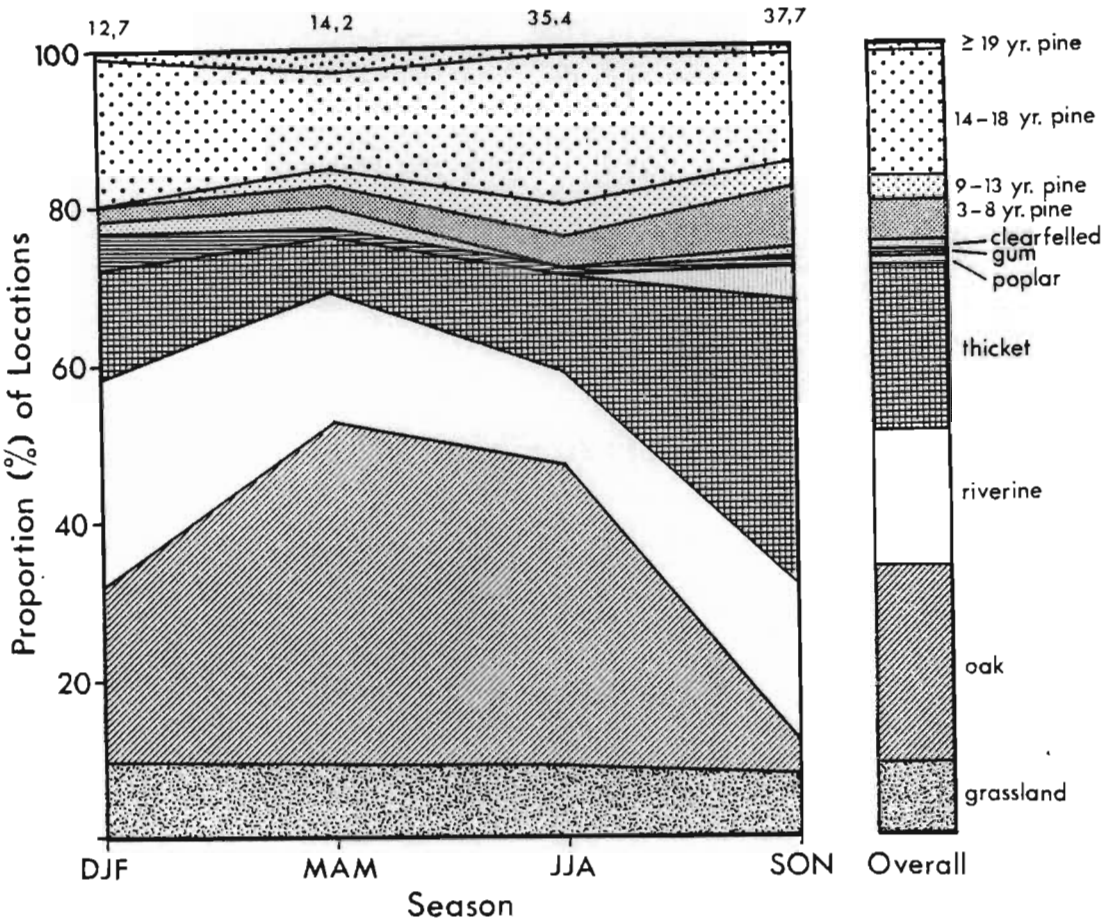


FIGURE 7.7 Seasonal variations in the nocturnal habitat utilization of marked female bushbuck at Weza. (Values at the top of the figure indicate the percentage of males monitored during that season, total number of locations = 858).

Overall, duiker were most frequently recorded in oaks (22,1%) clearfelled areas (20,7%) and 9-13 year pine stands (16,0%, see Fig. 7.8). None of the marked animals utilized indigenous forests, riverine areas, thickets, or gums and 19-30 year pines and poplars were rarely visited. Thus, as with sightings from censuses, duiker inhabited fewer habitat types than bushbuck, which is also reflected in their smaller relative niche width of 0,561. Duiker were recorded in only four habitats during summer, and of these 9-13 year pines and Mexican hawthorn were of greatest importance (34,6% and 30,8% respectively). Use of both these habitats declined in autumn

(Fig. 7.8) when duiker were located much more frequently in clearfelled (58,3%) and grassland (11,7%) areas compared to the previous season. Marked animals were found predominantly in oaks during winter (58,3%) although they were also monitored in young and intermediate aged pines (Fig. 7.8). While still an important habitat, use of oaks declined in spring (23,5%) when 9-13 year pines (19,6%) and cultivated areas (18,6%) were utilized with greater frequency than in winter. Relative niche width was greatest in spring (0,505) and declined to 0,303 in summer and 0,212 in autumn before increasing slightly to 0,218 in winter.

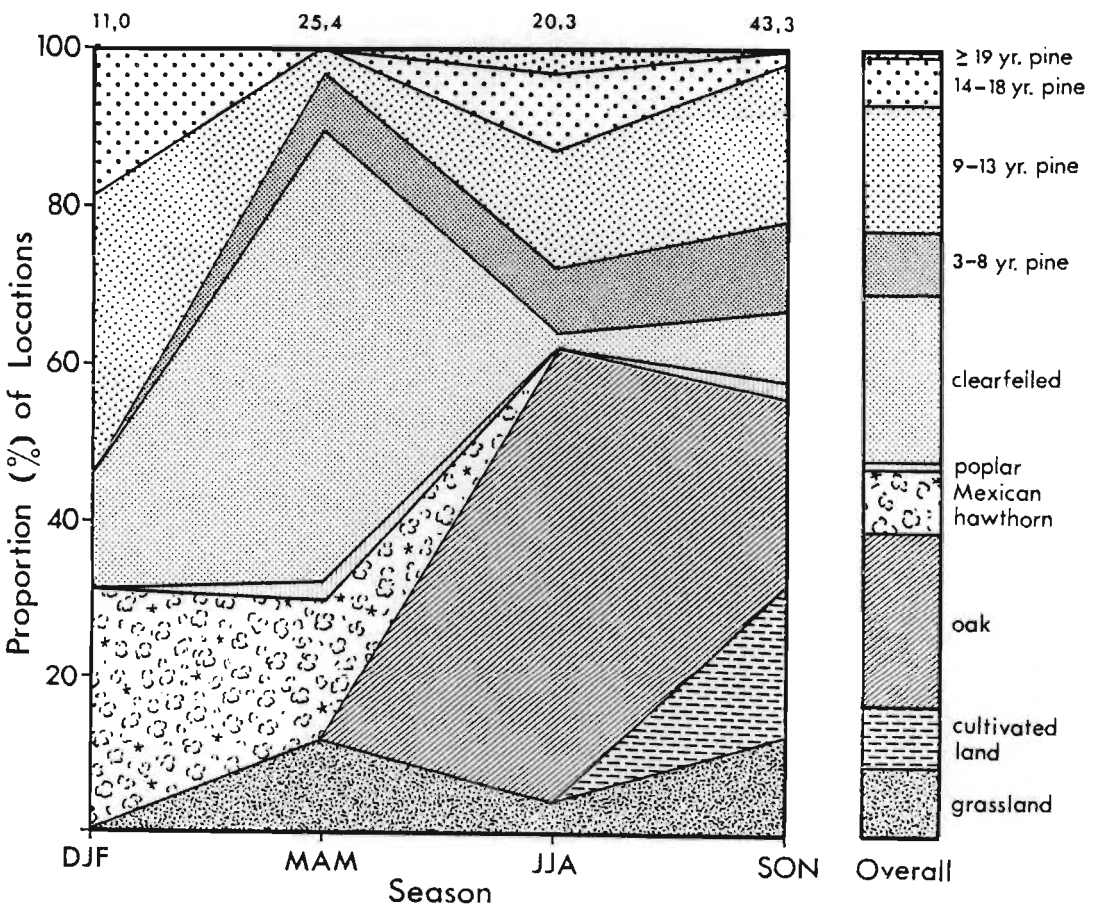


FIGURE 7.8 Seasonal variations in the proportions of marked duiker observed and monitored by radio tracking in the various habitat types at Weza. (Values at the top of the figure indicate the percentage of locations during that season, total number of locations = 425).

7.3.5.3 Overlap in habitat utilization

Considering all seasons, habitats utilized by all marked bushbuck and duiker overlapped by 49,2%, slightly higher than that estimated from census data. Oaks were the habitat most shared (15,8%) by these two antelope species. Greatest overlap occurred in winter (62,7%) and declined progressively during the remainder of the year with 38,9% in spring, 33,6% in summer (when the only habitats shared by marked bushbuck and duiker were pines) and 19,5% in autumn.

7.3.6 Habitat Selection

7.3.6.1 Bushbuck

In order to summarize habitat preference data, a composite home range was determined for all of the bushbuck that inhabited I.S.A.1. This composite home range was based on 3 409 individual locations (Fig. 7.9). Although habitat alterations occurred in this area during field work, these could not be updated and summarized without artificially increasing the actual area utilized by marked bushbuck. Consequently, the habitat map that was used for availability purposes reflected the condition of the vegetation as in August 1983 (Fig. 7.10). This period was selected since it fell approximately mid-way between the start (August 1982) and finish (October 1984) of intensive animal tracking and also represented the time when there were most marked animals in the intensive study area (although additional animals were marked after this time their numbers were partially offset by natural mortalities during the winter and early spring of 1983).

Habitats most preferred by bushbuck (irrespective of sex, time of day or season) were oaks, riverine vegetation and thickets. Over 50% of all bushbuck locations (determined from direct observations and from radio telemetry) were recorded in these three vegetation types which together accounted for 7,6% of the total study area (Table 7.3).

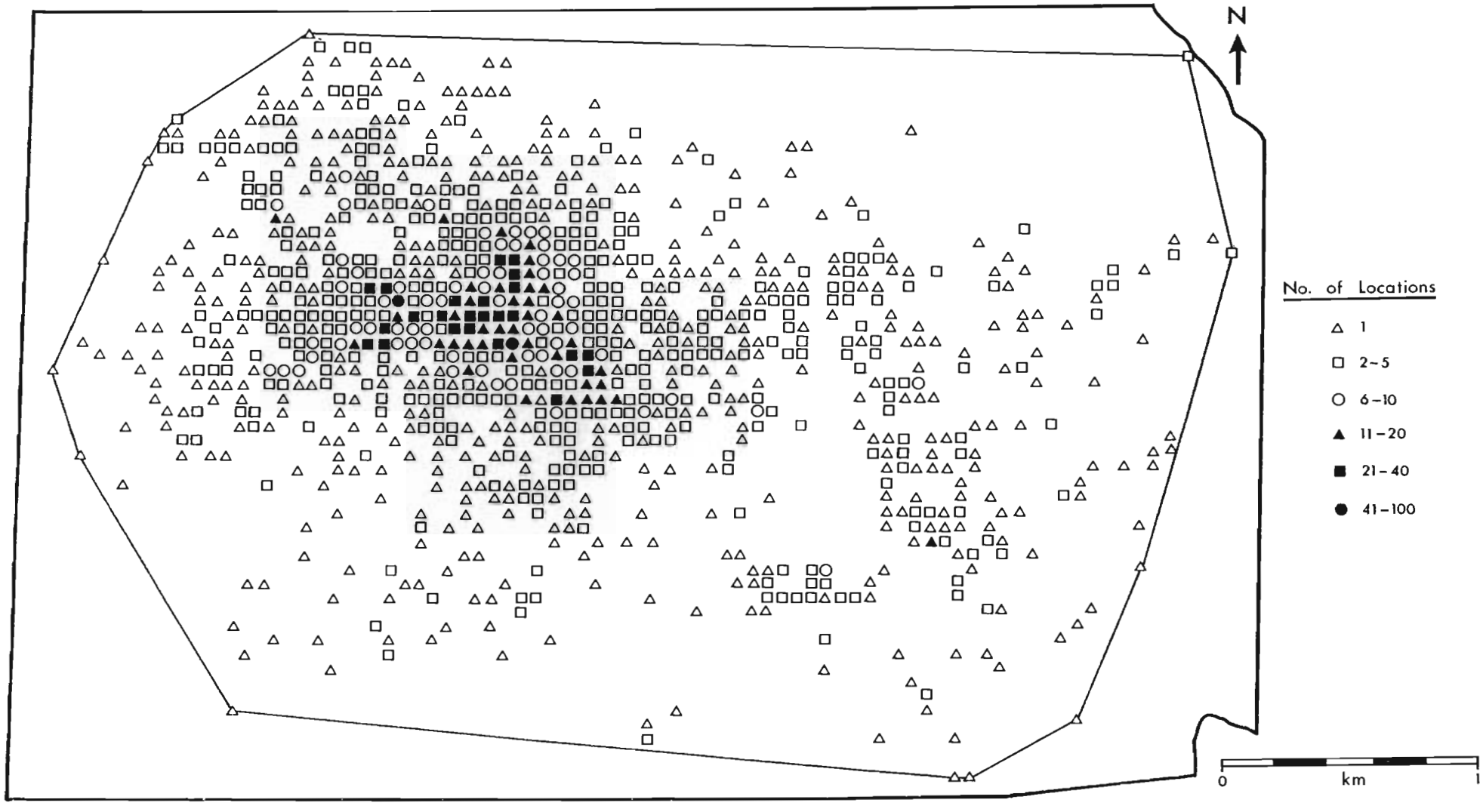


FIGURE 7.9 Distribution of marked bushbuck in I.S.A.1 located during the period from September 1981 to October 1984. (Total number of locations = 3409).

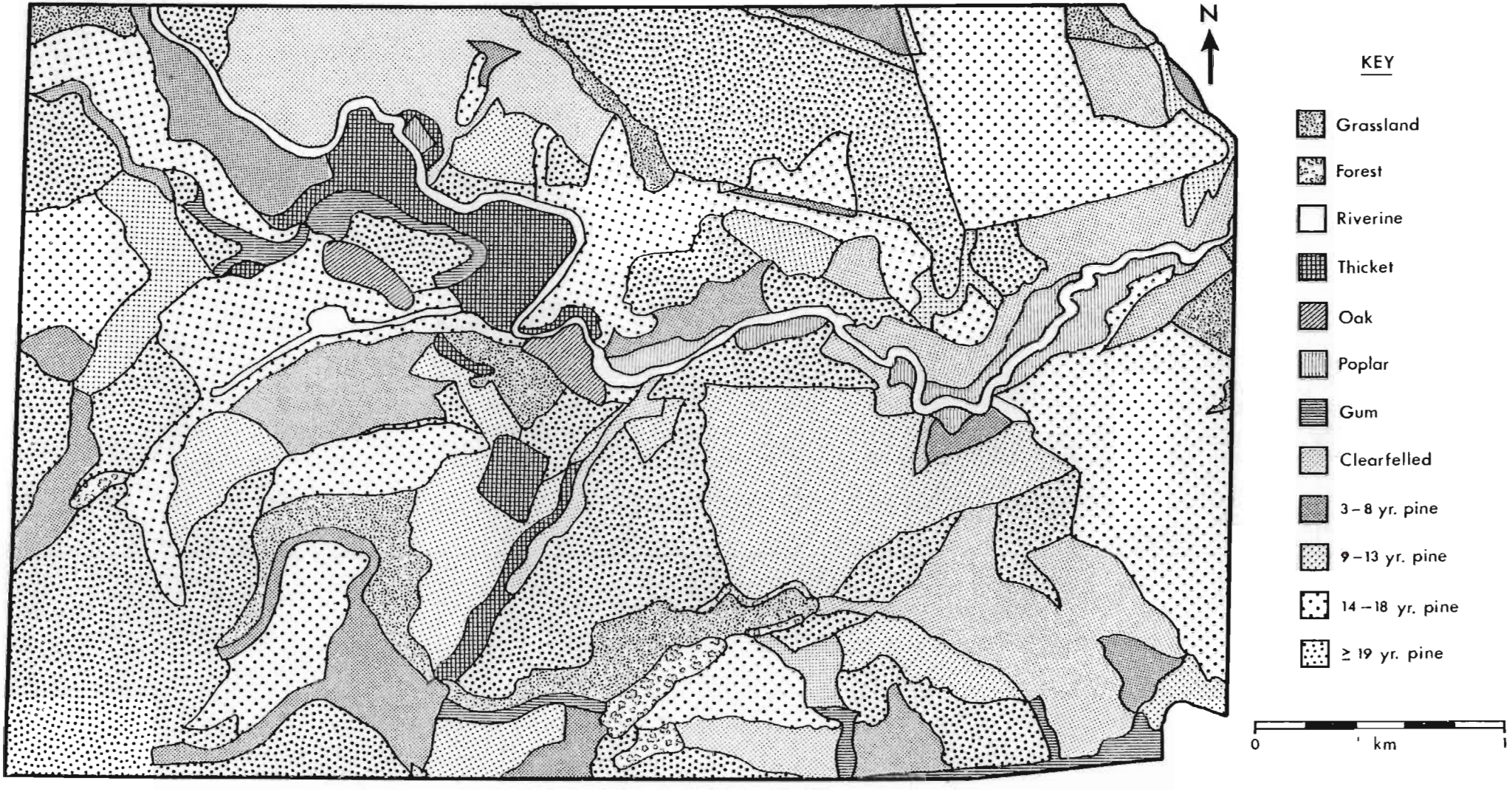


FIGURE 7.10 Habitat map of I.S.A.1 in August 1983.

TABLE 7.3 Habitat selection patterns of bushbuck as determined from the composite home range in I.S.A.1, listed in decreasing order of preference.

Habitat	Area(ha)	% of total area	No. of locations	% of total locations	H.P.I.	Exp. No. of locations	x^2	p
Oak	13,0	1,02	503	14,76	14,47	34,77	6305,42	< 0,001
Riverine	29,8	2,34	541	15,87	6,78	79,77	2666,83	< 0,001
Thicket	54,2	4,25	764	22,41	5,27	144,88	2645,70	< 0,001
Gum	19,9	1,56	57	1,67	1,07	53,18	0,27	n.s.
Grassland	64,1	5,02	156	4,58	0,91	171,13	1,34	n.s.
3 - 8 year pines	100,7	7,89	222	6,51	0,83	268,97	8,20	< 0,01
14 - 18 year pines	292,2	22,90	463	13,58	0,59	780,66	129,26	< 0,001
Poplar	29,0	2,27	46	1,35	0,59	77,38	12,73	< 0,001
9 - 13 year pines	200,2	15,69	251	7,36	0,47	534,87	150,66	< 0,001
Clearfelled	171,1	13,41	162	4,75	0,35	457,15	190,56	< 0,001
Indigenous forest	11,1	0,87	9	0,26	0,30	29,66	14,39	< 0,001
19 - 30 year pines	290,5	22,77	235	6,89	0,30	776,23	377,38	< 0,001
Total	1275,8	99,99	3409	99,99		3408,65	12502,74	< 0,001

Habitats used in proportion to their availability within the composite home range were gums and grassland areas, while 3-8 year pines were the least avoided of the remaining habitats (Table 7.3). Habitat preference indices were lowest for clearfelled areas, indigenous forests and 19-30 year pines, and as with 9-13 year and 14-18 year pines and poplar, all were significantly avoided by bushbuck. Identical trends in habitat selection/rejection were evident at the 5% level of significance when Bonferroni confidence intervals were employed (Table 7.4).

TABLE 7.4 Simultaneous confidence intervals using the Bonferroni approach for bushbuck utilization of the various habitat types at Weza.

Habitat type	Expected proportion of usage	Actual proportion of usage	95% confidence intervals	
			Lower	Upper
Oaks	0,010	0,148	0,129	0,167 *
Riverine	0,023	0,159	0,140	0,178 *
Thicket	0,042	0,224	0,202	0,246 *
Gum	0,016	0,017	0,010	0,024 n.s.
Grassland	0,050	0,046	0,035	0,057 n.s.
3 - 8 year pines	0,079	0,065	0,052	0,078 *
14 - 18 year pines	0,229	0,136	0,118	0,154 *
Poplar	0,023	0,013	0,007	0,019 *
9 - 13 year pines	0,157	0,074	0,060	0,088 *
Clearfelled	0,134	0,048	0,037	0,059 *
Indigenous forest	0,009	0,003	0,000	0,006 *
19 - 30 year pines	0,228	0,069	0,056	0,082 *

* - indicates a difference at the 0,05 level of significance

Data from males and females were analysed separately to determine whether habitat selection differed between the sexes during the day or at night. Methods of analyses were similar in that composite home ranges were constructed for

each sex and time period and the proportions of available habitats within each range were determined by planimeter. These results are summarized in Tables 7.5 and 7.6 (diurnal and nocturnal periods respectively). Almost identical trends were apparent between males and females during the day, with riverine areas and thickets being preferred and 9-13 year

TABLE 7.5 Diurnal selection patterns of (a) male and (b) female bushbuck as determined from composite home ranges in I.S.A.1, listed in decreasing order of importance.

	Habitat type	H.P.I.	X^2	p
a) Males	Riverine	2,71	83,17	<0,001
n=822	Thicket	2,41	144,57	<0,001
Area =	Indigenous forest	2,39	4,51	n.s.*
1888 ha	Oaks	1,89	10,53	<0,01
	Gum	1,73	6,23	n.s.*
	3 - 8 year pines	0,91	0,74	n.s.
	Poplar	0,89	0,13	n.s.
	Grassland	0,84	1,36	n.s.
	14 - 18 year pines	0,79	6,18	n.s.*
	9 - 13 year pines	0,75	10,95	<0,001
	19 - 30 year pines	0,66	14,28	<0,001
	Clearfelled	0,48	22,66	<0,001
b)Females	Riverine	2,71	126,58	<0,001
n = 881	Thicket	1,64	55,89	<0,001
Area =	Poplar	1,57	3,23	n.s.
873 ha	Grassland	0,98	0,02	n.s.
	Gum	0,94	0,15	n.s.
	14 - 18 year pines	0,94	0,53	n.s.
	Oaks	0,90	0,36	n.s.
	3 - 8 year pines	0,79	4,05	n.s.*
	19 - 30 year pines	0,48	25,73	<0,001
	9 - 13 year pines	0,46	26,31	<0,001
	Clearfelled	0,36	22,53	<0,001

* - $p<0,05$; see section 7.2.5.

pines, 19-30 year pine and clearfelled compartments avoided by both sexes (Table 7.5). Similar patterns of preference and avoidance were exhibited at night, with the exception that males used gums approximately in proportion to their availability while females avoided these trees (Table 7.6).

TABLE 7.6 Nocturnal selection patterns of (a) male and (b) female bushbuck as determined from composite home ranges in I.S.A.1, listed in decreasing order of importance.

	Habitat type	H.P.I.	X^2	p
a) Males	Oaks	8,90	1753,29	<0,001
n = 836	Thicket	1,87	47,03	<0,001
Area =	Riverine	1,75	19,93	<0,001
1600 ha	Clearfelled	1,18	2,18	n.s.
	Gum	1,11	0,09	n.s.
	Indigenous forest	1,00	0,00	n.s.
	Grassland	0,97	0,03	n.s.
	3 - 8 year pines	0,53	19,32	<0,001
	Poplar	0,49	10,10	<0,01
	9 - 13 year pines	0,48	58,88	<0,001
	14 - 18 year pines	0,42	40,74	<0,001
	19 - 30 year pines	0,36	46,66	<0,001
b)Females	Riverine	2,37	111,61	<0,001
n = 870	Oaks	2,26	135,88	<0,001
Area =	Thicket	1,22	8,54	<0,01
451 ha	Grassland	1,13	1,12	n.s.
	14 - 18 year pines	0,79	7,45	<0,01
	9 - 13 year pines	0,56	13,65	<0,001
	Clearfelled	0,54	2,98	n.s.
	3 - 8 year pines	0,52	20,06	<0,001
	Gum	0,33	17,78	<0,001
	19 - 30 year pines	0,10	69,63	<0,001
	Poplar	0,06	16,06	<0,001

All these results are somewhat surprising as bushbuck were frequently found in clearfelled areas (e.g. Figs. 6.1 and 7.5) while densities as high as 7 bushbuck/ha were estimated during capture operations in other indigenous forests at Weza. Comparisons were therefore made with results from Johnson's (1980) method to determine whether such anomalies might have resulted from inconsistencies in data collection or other sampling artefacts. Overall, habitat preference data determined from this ranking method resembled those calculated from % use:% availability ratios, with the exception that both natural forests and clearfelled areas were preferred habitats when analysed by the former method. Although used by comparatively few animals, indigenous forest was clearly the most preferred habitat, while clearfelled areas were selected over thickets on an annual basis (Table 7.7). As with % use:% availability indices, oaks and riparian vegetation were also preferred habitats, while poplars and pines over two years of age were generally avoided by bushbuck.

Since none of the marked female bushbuck located on a minimum of 10 occasions were ever recorded in indigenous forest (see 7.3.5.1.2), preference for this habitat was due entirely to selection by males, which was greater during the day than at night (Table 7.7). Similarly, both males and females exhibited a greater diurnal preference for 7 other habitats, of which riverine areas, thickets and gums could be considered as actively selected. Conversely, both sexes showed a greater selection for oaks, clearfelled and grassland areas, and 9-13 year pines at night than in the day, although 9-13 year pines were generally avoided by bushbuck at all times (Table 7.7).

Data from marked bushbuck indicated distinct trends in habitat utilization during the course of the year. Because Johnson's (1980) ranking method provided a ready means of summarising habitat preference data, and also yielded results more similar to those from general observations, this method was used exclusively for all seasonal analyses and comparisons.

TABLE 7.7 Overall habitat selection patterns of bushbuck at Weza as determined from Johnson's (1980) mean ranking method. (Habitats are listed in decreasing order of preference; positive values indicate preference, negative values indicate avoidance, figures in parentheses indicate the sample size where each animal was located on a minimum of 10 occasions).

MALES			FEMALES			M & F	
Night	Day	Overall	Night	Day	Overall	Overall	
3,00 (12)	4,00 (2)	2,43 (7)	4,50 (4)	1,60 (31)	1,33 (84)	2,43 (7)	Forest
2,42 (19)	1,00 (25)	1,41 (43)	1,04 (25)	0,82 (11)	0,98 (58)	1,16 (101)	Oak
0,82 (17)	0,50 (24)	0,94 (40)	0,69 (29)	0,30 (30)	0,26 (21)	0,96 (148)	Riverine
0,75 (2)	0,42 (13)	0,47 (64)	0,32 (14)	0,13 (20)	0,23 (80)	0,70 (61)	Clearfelled
0,50 (13)	0,37 (15)	0,46 (56)	0,24 (27)	0,07 (30)	0,00 (23)	0,32 (136)	Thicket
0,16 (22)	0,17 (24)	0,00 (30)	-0,37 (30)	0,03 (16)	-0,20 (53)		Grassland
-0,44 (9)	0,14 (22)	-0,01 (39)	-0,50 (16)	0,02 (24)	-0,25 (38)	-0,13 (77)	Gum
-0,50 (16)	0,09 (11)	-0,18 (52)	-0,64 (14)	-0,78 (9)	-0,28 (58)	-0,24 (110)	3-8 yr. pine
-1,08 (24)	-0,25 (18)	-0,45 (29)	-0,92 (19)	-0,80 (27)	-0,30 (84)	-0,25 (52)	Poplar
-1,17 (10)	-0,73 (15)	-0,47 (64)	-1,04 (14)	-0,81 (16)	-1,09 (60)	-0,38 (148)	14-18 yr. pine
-1,50 (11)	-0,82 (25)	-0,75 (65)	-2,50 (6)	-1,26 (25)	-1,16 (56)	-0,94 (121)	9-13 yr. pine
-1,53 (17)	-1,12 (25)	-1,14 (60)	No Data	No Data	No Data	-1,12 (120)	19-30 yr. pine

7.3.6.1.1 Habitat selection during spring

Overall, habitats most preferred by bushbuck in spring were indigenous forest, followed by clearfelled areas, oaks, riverine vegetation, thickets and grassland. Although both males and females showed a greater selection for clearfelled areas and oaks at night compared to day time, oaks were preferred more by males at this time of the year, while females actively selected fewer habitats of which riverine

areas were the most important (Table 7.8). Both sexes showed a greater selection for thickets during daylight hours than at night and use of indigenous forests by males showed a similar trend. Notable differences were evident between the sexes in their diurnal and nocturnal selection or rejection of several of the remaining habitats (e.g. gums, grassland, poplars and 3-8 year and 14-18 year pines, see Table 7.8). males consistently avoided pines aged between 3-13 years and 19-30 years as well as poplars, while females also rejected 9-13 year pines and 19-30 year pines, (although their avoidance of these habitats was not as strong as that shown by males) but showed a preference for 3-8 year pines during the day.

TABLE 7.8 Spring habitat selection patterns of bushbuck at Weza as determined from Johnson's (1980) mean ranking method. (See Table 7.7 for explanation of values).

MALES			FEMALES			M & F	
Night	Day	Overall	Night	Day	Overall	Overall	
4,38 (4)	4,00 (2)	2,43 (7)	4,75 (2)	0,89 (9)	1,40 (25)	2,43 (7)	Forest
2,92 (6)	1,29 (7)	2,08 (12)	1,85 (10)	0,56 (9)	1,13 (8)	1,17 (23)	Clearfelled
	1,13 (4)	1,20 (15)	0,54 (11)	0,38 (4)	0,65 (27)	1,11 (27)	Oak
0,75 (2) 0,75 (6)	0,83 (6)	0,72 (9)	0,33 (6)	0,14 (7)	0,33 (15)	1,04 (42)	Riverine
0,50 (3)	0,71 (5)	0,53 (15)	0,13 (8)	0,10 (10)	-0,10 (25)	0,61 (42)	Thicket
0,30 (5)	0,38 (4)	0,50 (17)	0,07 (7)		-0,25 (12)	0,12 (25)	Grassland
-0,10 (5)	0,25 (8)	0,46 (13)	-0,10 (5)	0,00 (2) 0,00 (9)	-0,60 (21)	-0,19 (26)	Gum
-0,50 (5)	0,07 (7)	-0,13 (15)	-1,42 (6)	-0,13 (4)	-0,68 (17)	-0,34 (45)	14-18 yr. pine
-0,75 (8)	-0,67 (6)	-0,48 (20)	-1,56 (8)	-0,17 (3)	-0,77 (15)	-0,45 (30)	3-8 yr. pine
-1,38 (4)	-0,86 (9)	-0,65 (20)	-2,00 (5)	-1,25 (4)	-1,20 (5)	-0,83 (35)	9-13 yr. pine
-1,79 (7)	-1,38 (4)	-1,27 (11)	-3,00 (2)	-1,75 (6)	-1,30 (15)	-1,25 (16)	Poplar
-2,83 (6)	-2,50 (8)	-2,53 (20)	No Data	No Data	No Data	-1,54 (41)	19-30 yr. pine

7.3.6.1.2 Habitat selection during summer

Habitat selection by bushbuck during the summer months included three vegetation types (poplar, gum and 3-8 year pine) that had been avoided in the previous season. Preference for poplars was largely a nocturnal event by both males and females, while females also exhibited a greater preference for riverine areas during nights (Table 7.9). The third most preferred habitat, oaks, was used more by females than males particularly during the day. Both sexes showed a greater preference for gums and 3-8 year pines at night, and a similar trend in thicket selection was evident from females

TABLE 7.9 Summer habitat selection patterns of bushbuck at Weza as determined from Johnson's (1980) mean ranking method. (See Table 7.7 for explanation of values).

MALES						FEMALES						M & F	
Night		Day		Overall		Night		Day		Overall		Overall	
3,25 (2)		1,44 (8)		2,00 (8)		2,50 (1)		2,15 (10)		1,68 (22)		1,51 (38)	Riverine
1,33 (3)		0,88 (4)		1,28 (16)				1,75 (4)		1,17 (9)		0,85 (17)	Poplar
1,00 (2)		0,38 (8)		0,17 (9)		1,00 (2)	1,00 (2)	0,71 (7)		0,97 (15)		0,44 (24)	Oak
0,83 (3)		0,07 (7)		0,15 (17)		0,70 (5)		0,50 (9)		0,44 (18)		0,31 (26)	Gum
0,50 (1)				0,00 (8)		0,67 (3)		0,20 (10)		0,37 (19)		0,26 (35)	3-8 yr. pine
0,13 (4)		-0,13 (4)	-0,13 (8)	-0,04 (14)				0,00 (11)		0,27 (24)		0,22 (41)	Thicket
		-0,21 (7)		-0,11 (7)		0,25 (2)	0,25 (2)	-0,23 (11)		-0,15 (10)		-0,28 (38)	14-18 yr. pine
0,00 (2)	0,00 (3)	-0,44 (8)		-0,13 (16)		0,00 (5)		0,50 (5)		-0,38 (24)		-0,32 (17)	Clearfelled
-0,83 (3)		-0,60 (5)		-0,44 (9)		-1,00 (2)		-1,17 (9)		-0,88 (8)		-0,36 (21)	Grassland
-2,25 (2)		-0,83 (6)		-0,55 (11)		-1,10 (5)		-1,25 (4)		-1,50 (18)		-1,27 (31)	9-13 yr. pine
-4,50 (2)		-1,00 (4)		-1,23 (15)		-2,75 (2)		-2,17 (9)		-2,29 (17)		-1,38 (33)	19-30 yr. pine
No data		No data		No data		No data		No data		No data		No data	Forest

but not males. Overall, although bushbuck were weakly associated with clearfelled areas, this habitat type was the most preferred habitat of both sexes during nights (Table 7.9). Males and females avoided 19-30 year pines at all times, and females consistently showed a greater avoidance of 9-13 year pines at this time. Other summer habitats of little importance to or generally rejected by bushbuck included grassland areas and 14-18 year pines.

7.3.6.1.3 Habitat selection during autumn

Although still preferred habitats, riverine areas and poplars declined in importance during the autumn months and were replaced by oaks and clearfelled areas, both of which received greater use by both sexes at night (Table 7.10). Poplars continued to be a preferred diurnal habitat for males and females, and although females showed a similar temporal preference for riverine areas, these were largely avoided by males which exhibited a greater preference for grasslands and thickets, particularly at night. Grasslands were also preferred by females at this time, but thickets were only important during daylight hours. Both sexes also showed a greater preference for 14-18 year pines during the day. Habitats totally or generally avoided by bushbuck during autumn were 9-13 year pines, 3-8 year pines (except by males during the day), gums and 19-30 year pines (which females were positively associated with during the autumn nights).

7.3.6.1.4 Habitat selection during winter

Overall, bushbuck showed a preference for only four habitats; oaks, clearfelled sites, riverine vegetation and thickets. Only two of these, oaks and riverine areas, were preferred by females, while males showed a weak preference for an additional vegetation type, grassland (Table 7.11). With the exception of riverine areas, males exhibited a greater preference for all these habitats at night compared to daylight use. Important habitats used by males during the

TABLE 7.10 Autumn habitat selection patterns of bushbuck at Weza as determined from Johnson's (1980) mean ranking method. (See Table 7.7 for explanation of values).

MALES			FEMALES			M & F	
Night	Day	Overall	Night	Day	Overall	Overall	
3,50 (2)	4,00 (1)	2,07 (7)	6,00 (1)		1,00 (10)	1,44 (17)	Oak
3,00 (4)	1,17 (3)	1,00 (6)	1,58 (6)	1,00 (6) 1,00 (3)	0,70 (5)	0,86 (11)	Clearfelled
1,50 (1)	0,75 (2)	0,88 (4)	1,17 (3)	0,38 (4)	0,65 (17)	0,27 (9)	Poplar
1,00 (3)	0,50 (2)	0,63 (12)	0,33 (6)	0,10 (5)	0,33 (6)	0,09 (31)	Riverine
-0,25 (6)	0,33 (3)	0,38 (8)	0,17 (3)	-0,25 (2)			Thicket
-0,40 (5)	0,00 (1)	0,33 (9)	-0,25 (2)	-0,30 (5)	-0,17 (12)	-0,17 (6)	0,05 (21) 0,05 (10) Grassland
-0,50 (2)	-0,50 (4)	-0,38 (4)	-0,63 (4)		-0,20 (5)	0,00 (25)	14-18 yr. pine
-1,17 (3)	-1,00 (2)	-0,57 (14)	-0,75 (6)	-0,5 (3) -0,5 (1) -0,5 (4)	-0,30 (10)	-0,03 (17)	19-30 yr. pine
-1,25 (2)	-1,33 (3)	-0,75 (8)	-0,83 (3)		-0,39 (9)	-0,65 (10)	Gum
-1,75 (2)	-1,50 (2)		-1,38 (4)	-0,63 (4)	-0,58 (13)	-0,81 (18)	3-8 yr. pine
-1,90 (5)	-2,00 (4)	-1,38 (12) -1,38 (4)	-6,00 (1)	-0,75 (2)	-0,85 (10)	-0,89 (22)	9-13 yr. pine
No data	No data	No data	No data	No data	No data	No data	Forest

day included gums and 3-8 year pines as well as riverine vegetation, oaks and thickets, while females also selected for 14-18 year pines at this time. In contrast to males, no females were located in clearfelled regions, and generally showed a greater preference for 9-18 year pines (Table 7.11). Although poplars were generally used more by both sexes during the day, this was the least utilized habitat at this time, while females showed a general avoidance of 3-8 and 19-30 year pines, grassland and gums and males generally rejected 9-18 year pines. Differences in habitat selection between the sexes were therefore probably greatest during this season.

TABLE 7.11 Winter habitat selection patterns of bushbuck at Weza as determined from Johnson's (1980) mean ranking method. (See Table 7.7 for explanation of values).

MALES			FEMALES			M & F	
Night	Day	Overall	Night	Day	Overall	Overall	
2,07 (7)	1,13 (4)	1,67 (15)	1,56 (9)	2,83 (6)	1,53 (18)	1,59 (33)	Oak
1,80 (5)	1,08 (6)	1,20 (10)	0,10 (5)	0,40 (5)	1,43 (20)	1,20 (10)	Clearfelled
1,25 (4)	0,63 (4)	0,80 (15)		0,30 (5)	-0,21 (17)	1,01 (37)	Riverine
1,10 (5)		0,53 (17)	-0,06 (8) -0,06 (8)	0,00 (5)		0,27 (32)	Thicket
0,36 (7)	0,50 (6) 0,50 (5)	0,09 (11)	-0,10 (5)	-0,17 (6)	-0,25 (14) -0,25 (14)	-0,26 (27)	3-8 yr. pine
-0,50 (7)	-0,17 (6)	-0,11 (9)	-0,18 (11)	-0,50 (2)	-0,30 (22)	-0,29 (21)	Grassland
-0,83 (3)		-0,15 (17)	-0,30 (5)	-0,83 (3)	-0,50 (12)	-0,33 (21)	Gum
-0,90 (5)	-0,33 (6) -0,33 (3)	-0,27 (13)	-0,50 (3)	-1,00 (4)	-0,70 (10)	-0,74 (40)	14-18 yr. pine
-1,25 (8)	-0,38 (4)	-1,08 (6)	-1,50 (3)	-1,17 (3)	-0,88 (4)	-0,79 (33)	9-13 yr. pine
-1,31 (8)	-0,50 (2)	-1,18 (19)	-3,50 (1)	-1,70 (5)	-1,88 (12)	-0,86 (29)	19-30 yr. pine
-1,83 (3)	-1,79 (7)	-1,28 (18)	No data	No data	No data	-1,00 (10)	Poplar
No data	No data	No data	No data	No data	No data	No data	Forest

7.3.6.2 Duiker

A composite home range was determined from 425 positions of 16 duiker each located on a minimum of 10 occasions. Habitat preference indices based on % use:% availability ratios calculated from this composite area of 401,8 ha indicated that duiker selected four habitats, namely Mexican hawthorns, oaks, grasslands and clearfelled areas (Table 7.12). Habitats used approximately in proportion to their availability were 9-13 year pines and cultivated areas, although earlier results (Fig. 7.8) indicate that duiker may exhibit a preference for these habitats during certain times

TABLE 7.12 Habitat selection patterns of duiker as determined from the composite home range method, listed in decreasing order of preference.

Habitat	Area(ha)	% of total area	No. of locations	% of total locations	H.P.I.	Exp. no. of locations	x^2	p
Mexican Hawthorn	2,1	0,52	34	8,00	15,38	2,21	457,29	<0,001
Oak	9,2	2,29	94	22,12	9,66	9,73	729,85	<0,001
Grassland	22,9	5,70	40	9,41	1,65	24,23	10,26	<0,01
Clearfelled	52,6	13,09	88	20,71	1,58	55,63	18,84	<0,001
9 - 13 year pine	72,1	17,94	68	16,00	0,89	76,25	0,89	n.s.
Cultivated land	40,8	10,15	34	8,00	0,79	43,14	1,94	n.s.
14 - 18 year pine	46,8	11,65	23	5,41	0,46	49,51	14,19	<0,001
Poplar	14,0	3,48	6	1,41	0,41	14,79	5,22	n.s.*
3 - 8 year pine	91,1	22,67	34	8,00	0,35	96,35	40,35	<0,001
19 - 30 year pine	31,8	7,91	4	0,94	0,12	33,62	26,10	<0,001
Riverine	4,3	1,07	0	0,00	0,00	4,55	4,55	n.s.*
Thicket	10,4	2,59	0	0,00	0,00	11,01	11,01	<0,001
Indigenous	3,7	0,92	0	0,00	0,00	3,91	3,91	n.s.*
Total	401,8	99,98	425	100,00		424,93	1324,40	<0,001

* $p < 0,05$ see section 7.2.5.

of the year. Habitats generally avoided by these antelope were poplars, riverine vegetation and indigenous forests ($p<0,05$) and duiker significantly avoided 3-8 year pines, 14-30 year pine and thickets ($p<0,001$, see Table 7.12). Gums did not occur within the duiker composite home range.

Oaks, grassland and Mexican hawthorns remained the most preferred duiker habitats when data were analysed using Johnson's (1980) ranking method, and were selected by every duiker that had these vegetation types within individual ranges. Cultivated land and 14-18 year pines were more favoured by duiker in this analysis, while clearfelled areas and 9-13 year pines declined in importance (Table 7.13). Individual selection was most varied for 3-8 year pines,

TABLE 7.13 Overall habitat selection patterns of duiker at Weza as determined from Johnson's (1980) mean ranking method. (Habitats are listed in decreasing order of preference; positive values indicate preference, negative values indicate avoidance. Sample sizes (n) only included those animals that were located on a minimum of 10 occasions).

Habitat type	Overall		Males		Females	
	n	$\bar{x}$ rank value	n	$\bar{x}$ rank value	n	$\bar{x}$ rank value
Oak	3	1,67	2	2,00	1	1,00
Grassland	7	1,36	4	1,25	3	1,50
Mexican hawthorn	5	1,20	3	1,00	2	1,50
Cultivated land	6	1,17	4	1,75	2	0,00
14 - 18 year pines	8	0,75	6	0,83	2	0,50
Clearfelled	10	0,20	6	0,67	4	-0,50
3 - 8 year pines	10	-0,45	7	-0,64	3	0,00
19 - 30 year pines	5	-0,80	3	-0,83	2	-0,75
9 - 13 year pines	10	-0,90	6	-1,17	4	-0,50
Poplar	6	-1,08	4	-1,25	2	-0,75
Thicket	2	-1,25	2	-1,25	0	N/A
Indigenous forest	1	-2,00	1	-2,00	0	N/A
Riverine	3	-2,33	2	-2,25	1	-2,50

while only one duiker showed a preference for areas of mature timber. All duiker consistently avoided poplars, thickets, forest and riverine areas. Consequently, habitat selection patterns were very similar for both sexes, the only notable differences being male selection for clearfelled areas (which were avoided by females) and rejection of 3-8 year pines which were generally used in proportion to their availability by females. Insufficient data precluded comparisons on a seasonal or temporal basis.

7.4 DISCUSSION

7.4.1 Habitat Utilization

7.4.1.1 Limitations of data collection and interpretation

Trends in habitat utilization were clearly influenced by the different areas surveyed and methods of data collection employed in this study. For example, levels of bushbuck utilization of oaks varied from 1,4% for the culled population, 24,0% for the censused population and 15,8% for the marked population (Figs. 6.1, 7.1 and 7.3 respectively). These results were obviously influenced by common as well as different sources of bias.

Since culling and census data were obtained from observations made from a vehicle, these probably overestimated the importance of habitats adjacent to roads and underestimated the importance of more remote areas (Bailey et al. 1983). Approximately half the data from marked animals would be biased in a similar manner. Although Phillips et al. (1973) concluded that their visual observations of collared moose were biased by habitat type and could not be used in range use analyses, the extensive network of roads at Weza certainly reduced, but not necessarily eliminated, such bias in this study. Several other studies have shown that ungulates may avoid habitats adjacent to roads and tracks (e.g. Lyon 1979; Rost and Bailey 1979; Carleson 1982), but few animals (particularly in

the intensive study areas) could have avoided such areas at Weza because of the high density of access areas and the mosaic of small but highly diverse vegetation types.

Differential visibility was undoubtedly another source of bias (Table 7.1) and due to largely ineffective spotlight penetration in densely structured habitats (e.g. thickets, riverine areas, young pine stands and indigenous forests), results from these vegetation types must be considered as underestimates. Data from marked animals would be less affected than those obtained from culling and census exercises as the former included locations determined from radio tracking. Further, seasonal fluctuations in vegetation growth clearly influenced ranges of visibility, which were least in summer and optimal in winter and early spring. Similar problems associated with differential visibility have been noted in numerous other studies of habitat utilization (e.g. Allen 1968; Martinka 1969; Zagata and Haugen 1973; Rounds 1981; McCullough 1982; Hanley 1983, 1984). Differences in seasonal ranges of visibility would be partially offset by management activities in timbered areas (see 7.3.2.1.) which occurred throughout the year, but these in turn would increase the variability within any one habitat type. Sage et al. (1983) recorded an increase in deer observation rates after timber harvesting, and suggested that this was due to both an increase in visibility as well as actual use. Weather conditions also influenced visibility, particularly in the rainy season when mist was fairly common at night (also see Irby 1982). Such conditions were generally avoided during observations of marked animals or during censuses but were often encountered during culling operations. Although fewer animals were seen in late spring, summer and autumn compared to the rest of the year, this was not entirely due to reduced visibility; fewer animals were seen even in open habitats. Movement studies (Chapter Eight) and diet analyses (Chapter Six) suggest that animals were more mobile and less dependent on localized food resources at these times.

Overall trends in habitat utilization were therefore

also biased in favour of the larger sample sizes obtained in winter and spring and should be interpreted accordingly. Seasonal differences in the sample sizes of culled animals were not as great, but the overall numbers of animals collected in this study were significantly smaller than the numbers of recorded locations. Telemetry data were also biased by the fact that the majority of animals were captured and fitted with transmitters in winter. Since the average field life of transmitters used in this study was 111 days (see Appendix D), this inevitably led to a much higher proportion of locations obtained during winter and spring, than in summer or autumn. Apart from this unequal distribution of radio equipped animals, radio tracking data were not subject to the same limitations as field observations, but instead had their own sources of bias (7.1.1.1 and Appendix D). Although every effort was made to reduce these, the accuracy and precision of bearings could not be tested on every occasion and locations were probably least reliable in densely structure vegetation and in the areas where the terrain was more rugged.

Results from this study were certainly influenced by other sources of bias. Both bushbuck and duiker were much more conspicuous at night than during the day, irrespective of whether they were marked or not. Collars containing reflective tape (see Appendix D) were more obvious at night than collars without these markings, (also see Bailey et al. 1983) while certain marked individuals were seen much more frequently than others. Only marked animals seen and/or radio tracked a minimum of ten times were included in these analyses in order to reduce this bias; any threshold value higher than this would have led to a substantially reduced sample size. Censuses were conducted before many animals were collared, and subsequent resighting data and results from other studies (e.g. Sage et al. 1983) suggest that many census observations must have been made on the same but unknown number of individuals at different times. By virtue of their considerable size differences, bushbuck were undoubtedly more conspicuous than duiker in most habitats, while monitoring by radio tracking was certainly more

successful in the former than the latter species. Finally censuses and locations of marked animals were confined to the intensive study areas, and although these were initially selected as being fairly representative of the entire plantation area (see Chapter Two), notable differences between these sites and the rest of Weza became apparent as the study progressed. For example, very few oak trees existed in the extensive study area (where culling took place) but these occupied 1,02% (13,0 ha) of I.S.A.1. In contrast, indigenous forests formed 0,87% (11,1 ha) of this study area but accounted for approximately 19% of the total area at Weza State Forest. As a consequence of these disparities, assessments of antelope use of oaks may be underestimated if they are based solely on data from the extensive study area, and overestimated if results obtained from marked animals are extrapolated to the entire area. Similarly, bushbuck use of indigenous forest may be much greater than that determined from the intensive study area where this habitat was poorly represented. Comparing use to availability reduces the magnitude of some of these problems but by no means eliminates them (see below). From this discussion it might appear more appropriate to give greater reliance to data obtained from the extensive study area since this region is considerably larger and therefore more representative of Weza State Forest. However, such data are unfortunately restricted by sample size and are based on shot animals (it was impractical to record habitat and other details of all animals seen during culling operations). Animals were only shot if they were conspicuous and presented a suitable target; this practice undoubtedly favoured the collection of animals in more open areas with greater ranges of visibility (see Fig. 6.1).

Although some of these limitations were accounted for in subsequent analyses, others were considered unavoidable due to the prevailing conditions at Weza. As a result, and because other sources of error not even considered here were probably present, any conclusions regarding trends in habitat utilization should be treated with caution. Despite differences in body dimensions and disparate sample sizes,

these results are probably best suited for comparative purposes between bushbuck and duiker; such data were collected in the same manner and at the same time and therefore presumably have common rather than different sources of bias. Finally, Marcum and Scott (1985) have demonstrated that annual utilization patterns may vary as a result of direct and indirect weather influences. Inadequate precipitation can result in plant desiccation and a decline in both production and the nutritional value of forage, while production is also correlated with pregrowing season precipitation. Under these conditions, Marcum and Scott (1985) found that elk concentrated in areas selected where succulent forage was still available. This study at Weza was undertaken during periods of below average rainfall (Chapter Two) and consequently utilization and selection patterns of bushbuck and duiker may have differed from those exhibited during years of higher precipitation.

7.4.1.2 Patterns of habitat utilization and habitat overlap

For convenience, bushbuck and duiker levels of habitat utilization are summarised in Table 7.14. (Data from marked individuals included diurnal as well as nocturnal locations, but usage determined from culling and census was based entirely on observations at night). Bushbuck consistently used four habitats (grassland, thicket, 3-8 year pines and 14-18 year pines) at levels exceeding 5,0% of all locations, but only two of these (grassland and 14-18 year pines) were consistently used at similar levels by duiker (Table 7.14). The only habitat regularly utilized by bushbuck at levels less than 5,0% was gums and although duiker showed a similar trend, this latter species also made little or no use of thickets, riverine areas and poplars. Duiker also exhibited relatively narrower niche widths than bushbuck irrespective of the method of data collection. These results therefore differ from most published accounts of habitat utilization by bushbuck and duiker since the latter species is generally regarded as inhabiting a wider range of habitats than bushbuck (see 7.1.2). The most plausible explanation for

TABLE 7.14 Variation in the levels of habitat utilization by bushbuck and duiker at Weza.

Habitat Type	% use by bushbuck determined from:			% use by duiker determined from:		
	Culled sample (n = 129)	Census (n = 503)	Marked sample (n = 3363)	Culled sample (n = 116)	Census (n = 400)	Marked sample (n = 425)
Grassland	13,2	8,0	5,3	21,6	56,5	9,4
Oak	1,6	24,0	15,8	1,7	0,5	22,1
Cultivated Land	N/A	24,0	N/A	N/A	10,3	8,0
Forest	4,7	N/A	0,3	0,0	N/A	0,0
Riverine	8,5	4,4	12,5	0,0	0,0	0,0
Thicket	10,9	5,1	22,3	0,0	0,0	0,0
Poplar	2,3	5,6	1,3	1,7	0,8	1,4
Gum	2,3	0,4	2,7	0,9	1,0	0,0
Clearfelled	24,0	7,6	3,9	19,8	3,8	20,7
3 - 8 year pine	13,2	9,7	7,9	16,4	4,8	8,0
9 - 13 year pine	7,0	1,9	8,7	6,9	3,3	16,0
14 - 18 year pine	9,3	7,9	14,4	11,2	9,5	5,4
19 - 30 year pine	3,1	1,6	5,0	19,7	9,8	0,9
Mexican Hawthorn	N/A	N/A	N/A	N/A	N/A	8,0

this observed difference is that more forest and timbered habitats are acceptable to bushbuck at Weza than they are to duiker. General levels of avoidance (as determined from coefficients of association) and comparatively little overlap in habitat utilization (with the exception of culled animal data which was certainly biased by visibility factors) support this conclusion. Despite their similar preferences for cover, Dunbar (1978) also noted little overlap (30,1%) in habitat utilization between bushbuck and duiker in Ethiopia, even though he only recognised three broad habitat categories.

Another possibility worthy of consideration is that bushbuck, by virtue of their more extensive use of habitats, competitively exclude duiker from certain areas. Inspection of such a possibility is best achieved by examining niche overlap between these two species, which may be determined from indices of forage overlap (Chapter Six) and similarities in habitat utilization. Multiplication of these indices presupposes that the niche dimensions involved are independent of each other ("product α"; May 1975 cited in Anthony and Smith 1977). Alternatively, the arithmetic mean of the separate indices can be used to determine niche overlap when the niche dimensions are interdependent ("summation α"; May 1975 cited in Anthony and Smith 1977). Since resource dimensions at Weza are probably neither completely dependent or independent (e.g. habitats may be utilized for their source of cover, food or both of these), summation α may be regarded as the upper limit of niche overlap and product α should be regarded as a conservative value. Individual and combined indices are presented in Table 7.15 by season and method of data collection. There are undoubtedly other niche dimensions (e.g. spatial distributions, a more refined classification of habitat types etc.) that may have resulted in greater or less ecological separation but these were not examined during the course of this study. Nevertheless, upper limits of niche overlap indices computed in this way never exceeded 50% even when based on the least reliable method of data collection (the culled sample). Although threshold values as to when the

TABLE 7.15 Indices of overlap in (A) food habits and habitat utilization and (B) combined niche overlap among bushbuck and duiker at Weza State Forest (see text for details).

	SEASON				
	Spring	Summer	Autumn	Winter	Overall
(A) INDICES OF OVERLAP					
a) Diet (see Chapter Six)	0,200	0,106	0,088	0,071	0,119
b) Habitat utilization - culled sample	0,528	0,745	0,623	0,679	0,697
c) Habitat utilization - censused sample	0,544	0,358	0,350	0,361	0,400
d) Habitat utilization - marked sample	0,389	0,336	0,195	0,627	0,492
(B) NICHE OVERLAP					
Culled sample - product α : a x b	0,106	0,079	0,055	0,048	0,083
Culled sample - summation α :(a+b/2)	0,364	0,426	0,356	0,375	0,408
Censused sample - product α : a x c	0,109	0,038	0,031	0,026	0,048
Censused sample - summation α :(a+c/2)	0,372	0,232	0,219	0,216	0,260
Marked sample - product α : a x d	0,078	0,036	0,017	0,045	0,059
Marked sample - summation α :(a+d/2)	0,295	0,221	0,142	0,349	0,306

potential for severe competition may occur are difficult to determine (Leuthold 1978c) these results suggest that competitive exclusion rarely, if ever, occurred. Indeed, the coefficients of association determined from census data were positive only during winter, and this association together with the high index of habitat utilization overlap determined from marked animals (Table 7.15) suggest quite the opposite i.e. that bushbuck and duiker were most sympatric at this time of the year. The potential for competition during winter was undoubtedly reduced by the least similar diets of these two species at the time when food resources were most restricted (Table 7.15 and Chapter Six). This potential for competition may have increased during other seasons (depending on which sets of data are considered, Table 7.15) but this is considered to be of negligible importance as a limiting factor at these times since food was probably superabundant (Chapter Six).

The narrower relative niche widths of duiker therefore suggest that this species is more selective than bushbuck for the habitats available at Weza. Similarly, the consistently

narrower relative niche widths of female bushbuck indicate that these were more selective than males; the latter also had considerably larger home ranges (see Chapter Eight).

7.4.2 Habitat Selection

7.4.2.1. Limitations of data collection and interpretation

Although utilization data may facilitate census design and aid in capture operations, siting of hiking trails or even the allocation of hunting areas, the value of such data is clearly dependent on the method of collection and the areas that are surveyed. The quality of these records will also obviously influence the reliability of conclusions regarding habitat preferences. In this study habitat availability measurements were confined to the intensive study areas and so trends in habitat selection were based on utilization data from marked animals. The following descriptions do not fully account for differential visibility, road access, disparate seasonal sample sizes, unequal numbers of locations for individual animals, variations in the accuracy of bearings obtained from radio tracking and the other problems and limitations detailed above, and should therefore be considered rather as approximations specific to a relatively small area of Weza State Forest.

Even though measurements of habitat preference were confined to the marked population, conclusions regarding which habitats were preferred or avoided by both bushbuck and duiker varied considerably depending on the type of analysis. For example, HPI values determined from composite home ranges indicated that indigenous forest and clearfelled areas were significantly avoided by bushbuck (Table 7.3 and 7.4) yet these were the first and fourth most preferred habitats respectively using Johnson's (1980) ranking method (Table 7.7). Similarly, clearfelled areas were the fourth most preferred habitat of duiker based on availability within the composite home range (Table 7.12) but duiker showed a weak

selection for clearfelled sites when data were analysed using the ranking method (Table 7.13). Since the utilization data used for duiker preferences were the same for both estimates of preference, this lack of agreement must be due to differences in the calculated proportions of available habitat.

Which method provides the more meaningful and reliable assessment of selection? As Johnson (1980) points out, the very fact that an animal has its home range where it does indicates that the individual has already made a selection. The importance of such a selection is ignored, or at least diluted, if availability is based on a composite home range. It is diluted even more if the biologist considers that the entire "study area" is available to that animal. And if this principle is accepted, what about habitats 2 km, 20 km or even 200 km away from the study area; are these not also theoretically available to the animal too? Obviously by confining availability estimates to a study area or composite home range, this provides a boundary for what must be measured. However, I contest that these limits have no biological meaning whatsoever, and that they are simply imposed for convenience. Nevertheless, artificially imposed boundaries delineating available habitat are extremely common in the literature (see section 7.1.1.2) and in several of these, conclusions other than those inferring a lack of distinct preferences or rejections (e.g. Kohn and Mooty 1971; Peek et al. 1976; Penzhorn 1982; Rounds 1981) may have been obtained if availability was measured at the individual animal level.

Broad estimates of habitat availability such as those obtained from composite home ranges or study areas are less suitable for animals with restricted ranges than for more mobile species. They are even less appropriate for animals exhibiting territoriality since by definition resources within one territory are usually for exclusive use and are therefore not available to most other conspecifics. As with earlier examples, this constraint does not appear to be fully recognised in the literature. All available evidence

obtained in this study indicates that both duiker males and females are territorial and exclude adults of the same sex from their individual ranges (see Chapter Eight). Consequently results obtained from availability measurements within individual ranges (Table 7.13) are considered to be much more reliable than those obtained by the composite home range method (Table 7.12). Furthermore, individual ranges may be much less affected by successional changes or management practices than an entire study area; individual analyses can therefore facilitate data interpretation when such changes occur.

In conclusion, there is a very strong argument for measuring habitat availability at the individual level, despite the obvious convenience of measurements from broader areas. But the researcher is still faced with the dilemma of how use:availability ratios should be analysed. It has already been shown that utilization and availability are rarely measured without error or bias. If few animals are monitored at any one time, individual preferences may be detailed, but then these too should be interpreted with caution as differences in individual habitat selection may vary considerably with common areas of occupation (e.g.Irwin and Peek 1983; Pierce and Peek 1984). If data are more numerous and are summarised as mean HPI values which have not been transformed in some way, these are biased because of the unequal range of indices of avoided habitats compared to preferred habitats (see 7.1.1.2). Furthermore, in order to test the hypothesis that vegetation types are used in proportion to availability, statistical tests must be applied to the raw data. If, for example, only two of 50 bushbuck home ranges included indigenous forest, the mean value of the availability of this habitat will be as meaningless as that obtained from composite home range or study area measurements. Therefore, comparisons between actual proportions of use and proportions of availability may well be misleading even at the individual home range level. Since a ranking of categories is all that can be expected from an analysis of usage relative to availability, these problems are best overcome by the method proposed by Johnson (1980).

In addition, such a method is relatively insensitive to the inclusion or exclusion of dubious categories. The method is therefore particularly suited to conditions at Weza, because of the questionable inclusion of utilization data when habitats changed from one category to another (although these posed less of a problem when analysed on a seasonal basis of less duration). With the exception of Rounds (1981), no reference could be found concerning the influence that successional changes or management alterations might have on habitat selection analyses, yet such changes must be fairly common in many forested areas. Failure to recognise a) these influences and b) the numerous limitations associated with the collection and interpretation of utilization and availability data demonstrate that the development of theoretical aspects of habitat selection has indeed lagged behind other fields of behavioural ecology, as suggested by Partridge (1978) cited in Duncan (1983).

7.4.2.2 Selection and the functional role of habitats

The proportional use:availability indices presented in this study were included to demonstrate the wide assumptions that must be made with this method as well as its inherent limitations. Results obtained from such indices are considered much less reliable than those obtained from the ranking method, and this discussion is confined to assessments of habitat preferences and avoidances as obtained from the latter technique (i.e. Tables 7.7. to 7.11 and 7.13). Although such results are not accompanied by statistical tests of significance (largely because of the limitations of utilization and availability data collection) they nevertheless are suitable for comparative purposes. The overall results of this study correspond to Johnson's (1980) third-order of habitat selection. Higher levels of selection were evident from comparisons between the sexes of both bushbuck and duiker, seasonal selection within each home range (which also varied seasonally in size and was accounted for in subsequent analyses) and differences in diurnal and nocturnal habitat selection (due to inadequate sampling,

seasonal and diurnal differences could not be examined in either male or female duiker). However, because the results of this study did not provide any direct evidence of the various animal activities within each vegetation type, the functional significance of each habitat could not be ascertained. Indeed, Collins and Urness (1983) state "In practice, it is extremely difficult to assemble all information pertinent to an explanation of any one example of habitat selection". The approach probably best suited to providing an explanation of habitat selection or rejection would involve multivariate statistical techniques which in turn would require much more refined data collection methods than those used in this study (although these too would have attendant logistical problems in areas such as Weza and would necessitate a separate, highly specialised study). The functional role of selected habitats is therefore not easily determined (also see Gilmer et al. 1975; Nudds 1980; Cederlund 1983; Hanley 1983; Irwin and Peek 1983; Pietz and Tester 1983) and although the following discussion, in conjunction with findings of other herbivore-habitat relationships in similarly timbered areas, implies the functional importance of certain habitat types, it should be stressed that such implications are in certain instances, largely conjectural.

a) Bushbuck

In addition to the obvious food resources bushbuck need, all previous studies and general accounts stress the importance of cover to this species (see section 7.1.2.1). Since bushbuck are predominantly browsers at Weza, those habitats that offer canopy as well as lateral cover should be highly sought after by this antelope, since they presumably provide food as well as means of concealment (Mentis 1973b). The habitat most likely to provide these requirements is indigenous forest. Unfortunately little indigenous forest was available to the bushbuck marked in this study and was included in only four male bushbuck ranges during the spring. Despite this paucity of data, results indicate that indigenous forest is indeed the most preferred habitat at

Weza. Indirect evidence from capture operations where densities as high as 7 bushbuck per hectare were recorded in forests support this conclusion. Of the remaining habitats available to bushbuck in the study area, thickets and riverine areas were most similar in vegetation structure and species composition to natural forests, although both thickets and riparian vegetation contained an increased but variable element of exotic species. These too were highly preferred bushbuck habitats and overall ranked fifth and third respectively (Table 7.7). Ranked values indicated a general preference for both these habitats throughout the year, although thickets were not preferred by females during autumn and winter, while riverine areas were not a preferred habitat of males in autumn. However, a more interesting trend is apparent when diurnal selection is compared to nocturnal preferences. With few exceptions, which were never exhibited by both sexes during any one season, indigenous forests, thickets and riverine areas were preferred more during the day than at night. A similar trend of bushbuck preference for habitats with greater cover during the day has been noted by Waser (1975a) and Okiria (1980). The former author concluded that bushbuck were no more active at night than during the day, but that use of completely separate areas of cover during daylight hours was an antipredator strategy. Such striking differences in areas used by bushbuck were not evident in this study, although results of activity analyses were similar to those of Okiria (1980) in that feeding activities were much more pronounced at night, when bushbuck were usually much more mobile (see Chapter Eight). Since the time bushbuck spent feeding during the day was approximately half that of nocturnal foraging, this indicates that bushbuck preference for dense vegetation during the day is primarily due to the cover that such habitats provide and therefore may well have antipredator functions.

Since the dominant nocturnal activity of bushbuck at Weza was feeding, and animals were lying or standing motionless for half the time that they did during the day (see Chapter Eight), it is reasonable to assume that the

habitats most preferred at night would primarily be selected for foraging. Nocturnal habitats most preferred by both males and females included clearfelled areas, oaks and grassland, in addition to the densely structured habitats previously mentioned where selection was generally greater during the day. With the exception of male preferences of grassland during the spring, and female preference of oaks in summer, selection for all three of these habitats was consistently greater during hours of darkness than during the day. Bushbuck preference for oaks was most pronounced in autumn and winter; at these times this was overall the most preferred habitat of both males and females. The timing of this selection, coincided with the availability of the annual acorn crop, and since oak stands were devoid of any understory, there can be little doubt that such areas were actively sought for this rich source of food (see Chapter Six). Food availability in clearfelled areas undoubtedly fluctuated less during the year, although availability was directly influenced by silvicultural activities and the quality of food in this early successional vegetation probably altered significantly during the year. Nevertheless clearfelled areas were consistently the most preferred nocturnal habitat of both males and females throughout the year except winter, at which time males exhibited a greater selection towards oaks and thickets while none of the female winter home ranges included clearfelled sites. Possible reasons why bushbuck showed such a strong preference for such areas are considered below. However, it is interesting to note that although the average height of this early seral vegetation exceeded the mean height of understory vegetation in riverine areas (Table 7.1), clearfelled sites were invariably avoided during the day by both sexes throughout the year. The most obvious difference between these two habitats, apart from forage density, is the absence of canopy cover in clearfelled areas, suggesting that lateral cover alone is inadequate for bushbuck during the day (also see Odendaal and Bigalke 1979b). Bushbuck selection for grassland areas was much less pronounced than these other favoured nocturnal habitats, and was least preferred in summer. Both sexes showed a preference for grassland at

night during autumn, perhaps in response to recently burnt areas which served as fire breaks, and although this trend was continued by males in winter, grassland became a preferred habitat during the day in spring. Female bushbuck tended to avoid such areas in winter, but resumed selection at night during spring. These patterns of selection generally coincide with the periods when grass was most utilized by bushbuck (as determined from rumen analyses, see Chapter Six) although forbs may also have been consumed in such areas. Although cultivated land was not available to marked bushbuck, utilization data from bushbuck observed during censuses suggest that this habitat would also be a preferred nocturnal habitat where available, particularly during autumn and winter (Fig. 7.1).

These results therefore corroborate those of both Waser (1975a) and Okiria (1980) in that bushbuck utilization of more open areas for feeding purposes is much greater at night than during the day. They also demonstrate that conclusions regarding habitat utilization and/or selection in this species may be quite misleading if these are entirely based on data obtained only during periods of daylight or darkness (examples of the latter are culling and census exercises) when animals are least and most active respectively.

Consideration so far has been given to habitats most selected by bushbuck; only one of these contained planted timber. All of the remaining six habitat categories considered available to marked bushbuck are intensively managed by Forestry and consist of four different age classes of pine stands and two habitats dominated by hardwoods (poplar and gum). These accounted for 91% of the plantation area and approximately 46% of the total area at Weza in 1982 (see Chapter Two).

Pines in the age class of 3-8 years were the most preferred (or least avoided) of the remaining successional stages of conifers, and ranked 8th overall. Ranked values for this habitat were highest in summer followed by winter and during these periods 3-8 year pines were the 5th most

preferred habitat at Weza. No other categories of pine were ever among the top six most selected habitats of both male and female bushbuck at any time of the year. Both sexes showed less avoidance of 3-8 year pines during the day except in summer when this trend was reversed for both males and females. In contrast, bushbuck generally exhibited less avoidance of 9-13 year pines at night than during the day, with the exception of females in summer and autumn. Interestingly, mean ranked values for this habitat were never positive for either sex at any time of the year, and its overall ranked position was 11th (i.e. the 2nd most avoided habitat overall). The two other softwood habitats, 14-18 year pines and 19-30 year pines, were overall ranked 10th and 12th respectively. As with 3-8 year pines, 14-18 year pines were always preferred more during the day, except in spring when females preferred this habitat at night. The most avoided habitat at Weza, 19-30 year pines, were generally avoided less at night than during the day, although both males and females showed less avoidance during daylight hours in spring, and this trend was continued by females into summer.

Thus of the five successional stages created by forestry management, only the earliest seral communities associated with clearfelled areas were selected by bushbuck, and then only at night. A similar preference for early seral plant communities is shown by cervid populations in North America and Europe, where these are invariably selected as foraging areas (e.g. Nixon et al. 1970; Hooven 1973; Davis et al. 1977; Ffolliott et al. 1977; Papageorgiou 1978b). The value of such openings may depend on their size however, with large areas devoid of any substantial cover often being less utilized or preferred than smaller patches largely because of the proximity of cover in the smaller areas (e.g. Short et al. 1977; Bloom 1978; Papageorgiou 1978b; Lyon and Jensen 1980; McNicol and Gilbert 1980; Irwin and Peek 1983; Loft and Menke 1984; Sweeney et al. 1984). Consequently, the shape of the clearfelled areas may also be important, with long but narrow openings frequently considered preferable to more uniform shapes (e.g. Halls 1973a; Witmer and deCalesta 1983;

Loft and Menke 1984). An additional factor that may influence selection is the age of the clearfelled area. Recently felled areas are usually less attractive to cervids, possibly as a result of the lower plant biomass, the residual slash or disturbance activities associated with felling (Wallmo 1969; Regelin and Wallmo 1978; Lyon and Jensen 1980; Witmer and deCalesta 1983). Finally, the extent to which clearfelled areas may be used by cervids may also be influenced by the juxtaposition of openings of different age, and the spatial relationships between clearfelled areas and the surrounding habitats, including possible "edge effects" which are discussed later. With the exception of the effects of human disturbance (see Chapter Eight) none of these influences were considered in any detail during the course of this study on habitat selection. The category of clearfelled areas therefore included all logged areas irrespective of size or configuration from the time of felling until pines were two years old. The age at which such areas became less attractive to bushbuck was not determined and any beneficial effects of such habitats where pines exceeded two years of age would have been attributed to the next successional stage. Furthermore, no consideration was given to the silvicultural practices which inevitably affected both forage and cover availability in these compartments; such activities as cleaning by slashing or herbicidal treatments were more pronounced and frequent in this habitat than any of the other timbered categories (see Chapter Two). As a consequence of these influences and variables, it is highly unlikely that bushbuck use of clearfelled areas was consistent at all times and in all compartments containing this vegetation type and therefore the broad methods of data collection used in this study probably resulted in an underestimate of bushbuck selection for early seral communities.

Measurements of ground layer and understory vegetation indicated an inverse relationship between plant height and successional stage, with the most mature pine compartments having the least understory (Table 7.1). A similar relationship existed between mean ranked preference values and plant successional stage in timbered habitats, with the

exception that 9-13 year pines were generally more avoided than 14-18 year pines. These results infer that bushbuck preferences for pines were intimately associated with the level of cover and/or food available in these habitats. Both cover and food resources would be seriously altered by cleaning which usually occurred prior to thinning. Such thinning activities provided convenient junctions between the upper age of one habitat category and the lower limit of the next successional stage. Any negative effects of cleaning and thinning would therefore be included in selection or rejection assessments of the older of the two habitats. The one age class of pines not affected by thinning activities was 3-8 year pines, which interestingly were the least avoided of the established areas of plantations. Nevertheless, such compartments were usually cleaned prior to pruning, but this was usually conducted when trees were 6 or 7 years old. Thus unlike the other timbered compartments, 3-8 year pines were largely undisturbed until they approached the next successional stage. Furthermore, many of the attractive properties of clearfelled areas probably continued to exist in the younger compartments of this habitat, and these together with a largely undisturbed understory may have accounted for the selection bushbuck occasionally showed for this community. Pruning also occurred in the next category of pines when trees were 8 to 10 years old, and again between the ages of 10-12 years. This was the only habitat where trees were pruned twice as well as thinned, which meant that understory was usually removed three times in five years. It might be speculated that these cleaning activities accounted for the fact that 9-13 year pines were more avoided than 14-18 year pines, although measurements of plant regrowth after cleaning suggest that any detrimental effects were not very prolonged.

It is however, highly improbable that bushbuck avoidance of established plantations was due solely to the management practices of cleaning, pruning and thinning. On the contrary, such activities may indeed by beneficial to ungulate populations inhabiting forested areas (see below). The most likely reason for such avoidances concerns the

reduction of food and/or cover as the canopy of the overstory closes. Numerous North American studies have been made of this negative correlation between tree density or canopy cover and the availability of forage (e.g. Gaines et al. 1954 and Halls et al. 1956 both cited in Young et al. 1967; Baskett et al. 1957, Clary and Ffolliott 1966 and McConnell and Smith 1970 all cited in Wallmo et al. 1972; Halls 1974 cited in Conroy et al. 1982), and many of these have been quantified by measurements of forage or understory production (e.g. Young et al. 1967; Halls 1973b; Deschamp et al. 1979). Upon canopy closure, understory vegetation and hence forage usually remains sparse until trees are thinned or clearfelled (Blair and Enghardt 1976 cited in Blair et al. 1977) at which time competition for light, moisture and nutrients is reduced (Blair and Brunett 1980). Quantified studies of understory vegetation have invariably shown that plant production is greater in thinned than untreated stands of comparable age (e.g. Murphy and Ehrenreich 1965; McCulloch 1966 cited in Short et al. 1977; Behrend and Patric 1969; Nixon et al. 1970; Crawford 1971; Knierim et al. 1971; Blair and Feduccia 1977; Blair and Brunett 1980; Conroy et al. 1982; Monthey 1984) although understory browse production may decline quite rapidly as individual plants can grow vigorously and form a midstory component of little value to the foraging ungulate (Blair 1967; Crawford 1971; Blair and Feduccia 1977). Subsequent removal of this midstory element by cleaning may stimulate understory production more palatable to ungulates (Della-Bianca and Johnson 1965; Lawrence and Biswell 1972) but may also result in a reduction of cover.

Although detailed measurements of understory production were not maintained throughout the year in this study, measurements recorded in January 1982 (Table 7.1) and the selection patterns of bushbuck indicate that any stimulation in plant growth afforded by thinning etc. was relatively short-lived, possibly because the dominant pines themselves responded rapidly to such reductions in canopy cover (which after all, is one of the main objectives of thinning, see Chapter Two). Since 3-8 year pines and 14-18 year pines were usually avoided less during the day than at night, this might

suggest that such compartments provided more cover than nutritional value. Conversely 9-13 year pines were generally less avoided by bushbuck at night and these areas might have afforded relatively greater quantities of forage in response to the more intensive management of this category of pines. Cleaning operations in older stands may have limited browse availability since woody plants under a closed canopy sustain greater mortality of defoliated stems and are less likely to refoliate than those in open sites (Giese et al. 1964 cited in Miquelle 1983). Finally, pine compartments older than two years were more abundant than any of the other habitat categories, and although such compartments were usually relatively small and patchy, they collectively constituted 70% of the intensive study area. Since habitat requirements or preferences of bushbuck differed between day and night, this presumably resulted in localised movements through a mosaic of heterogeneous habitats. Consequently, an unknown proportion of bushbuck locations in the most common habitat types, which were not preferred areas, may have been recorded during such times of travel. This incidental use may have overestimated the importance of older pine habitats to bushbuck.

In summary, the striking contrast between bushbuck selection for early seral communities and their general avoidance of all later successional stages indicates that the principal value of pine habitats at Weza is confined to clearfelled areas which are important sources of forage. The quality of available forage may well be higher in such open sites compared to that of browse under pines or other dominant trees with a closed canopy (de Vos 1962 cited in Krefting 1974b; Halls and Epps 1969; Klein 1970; Deschamp et al. 1979) although other studies have detected little difference in browse quality in areas with open and closed canopies (Regelin et al. 1974; Conroy et al. 1982). Nevertheless, clearfelling results in a tremendous increase in the plant production of ground layer vegetation, while the species composition of clearfelled sites may alter dramatically due to the invasion of pioneer species once soil disturbance has occurred and competitive influences have been

removed. Because of this dramatically increased production and species diversity (see Law 1966; Halls and Alcaniz 1968; Crawford and Harrison 1971; Halls 1973b; Short et al. 1977; Regelin and Wallmo 1978; Stransky and Halls 1980) ungulates frequently spend a disproportionately large amount of time in clearfelled areas (e.g. Wallmo 1969; Wallmo et al. 1972; Regelin et al. 1972; Krefting 1974b; Monthey 1984) and may obtain a substantial portion of their nutritional requirements from such sites (Regelin et al. 1974; Peek et al. 1976). In addition to increased production, plant growth may also be initiated at an earlier age in open areas (Halls and Alcaniz 1968; Halls 1973b) which may thus become of primary importance during early spring following winters where food resources have declined to critical levels (see Table 7.8).

In general, gum plantations were more preferred by bushbuck than 3-30 year pine compartments. These were usually selected more during daylight hours although no obvious patterns of selection were evident when seasonal preferences were compared between males and females except in summer when gums were the fourth most preferred habitat and when both sexes showed a stronger selection at night. Due to an absence of any recent planting or thinning, all gum habitats consisted of mature trees with largely undisturbed understories, which when dense, consisted largely of regenerating seedlings and saplings. Overall, gums were most preferred during the summer months when they were the fourth most preferred habitat used by bushbuck. The only other time when these trees were preferred by both males and females was during daylight hours in spring; rumen analyses revealed that gums were only eaten by this antelope during late winter and spring, with a peak in September and October (see Fig. 6.13). These results suggest that gums were utilized both for the forage and cover they provided but that bushbuck were generally attracted to alternative habitats. Where understory was sparse, this was probably due to the same principal factor affecting understory growth in pine plantations, i.e. diminished light intensities resulting from canopy closure.

Bushbuck selection for poplars varied during the year, but both sexes exhibited the same patterns of preference. Poplars were consistently preferred more during the day, and assumed much greater importance in summer and autumn but were avoided during winter and spring. Together with oaks, these were the only deciduous habitats. Consequently, canopy cover was present for much of the year but absent in late autumn, winter and early spring, due to leaf abscission (bushbuck were excluded form compartments of younger poplars by electric fencing). These trends, together with an obvious avoidance of clearfelled areas during the day, suggest that bushbuck requirements for diurnal habitats include extensive overstories. Bushbuck may also have avoided poplar areas in winter and spring as a result of the copious leaf litter at these times, which tended to bury ground layer vegetation and make silent access through such compartments virtually impossible. Poplars were always in close proximity to water courses which may have provided an additional source of attraction (e.g. Simpson 1974a) although the relatively few animals that included poplars in their home ranges suggest that bushbuck were by no means dependent on such areas. Wigley et al. (1980) found little difference between day and night use in even-aged poplar plantations by white-tailed deer, but these deer showed a much greater preference for perimeter areas adjacent to natural forest both on a daily and seasonal basis.

These findings introduce another factor that may well have influenced habitat selection by bushbuck, namely the use of ecotones. Such areas are commonly considered to be of value to wildlife since there is a tendency for increased diversity and density of community junctions; this is commonly referred to as the "edge effect" (Odum 1971). Forest edge, especially that obtained from clearfelling, may be utilized more than other habitats by cervids and other wildlife (Reynolds 1962, 1966; Julander and Jeffery 1964 and Harper 1969 all cited in Hanley 1983; Willms 1971 cited in Kirchhoff et al. 1983; Lindzey and Meslow 1977; Cairns and Telfer 1980; Lyon and Jensen 1980; Clark and Gilbert 1982; Witmer and deCalesta 1983; Loft and Menke 1984). Preference

for edge probably results from the close proximity of cover and forage areas (Thomas et al. 1979b cited in Hanley 1983) or when snow depths make more open areas inaccessible (Brusnyk and Gilbert 1983). Increased use of edge is not always apparent however (e.g. Kirchhoff et al. 1983) nor need it be exhibited at the edge itself but some distance away from the juxtaposition of two habitats (Hanley 1983). The phenomenon of edge was not investigated in this study because it could not be examined in sufficiently fine detail (also see Clark and Gilbert 1982) using the existing methods of data collection. (Habitat use was recorded as the dominant vegetation occurring with the 60 m x 60 m grid where radio bearings intersected. Since the average size of compartments in the intensive study area was 7,0 ha (Chapter Two) and assuming these were square in shape, then edge as measured by a 60 m belt around the perimeter would constitute 70% of the total compartment. The proportion of "edge" would be even greater in compartments of irregular shape). Although edge was abundant at Weza due to the mosaic of successional stages created by intensive forest management and small patches of unmanaged habitats (Fig. 7.9), its effects and utilization are probably much more pronounced at junctions of extensive but highly diverse habitats.

So far, habitat selection patterns of bushbuck have been considered in terms of the functional importance of the availability of food and cover. As has been shown, it is difficult to separate these two requirements since some habitats undoubtedly provide both simultaneously, while in others it is not immediately apparent which commodity is the greater source of attraction (also see Suring and Vohs 1979; Henry 1981; Penzhorn 1981; Rounds 1981). Although previous studies demonstrated the importance of food and cover to both bushbuck and forest wildlife (section 7.1.2.1; Davis 1977; Nudds 1980; Cederlund 1983; Monthey 1984) it would be naive to assume that these are the only factors of any functional significance influencing habitat selection.

Earlier, reference was made to the distinct preference bushbuck show for habitats close to permanent water supplies,

while other authors have remarked on the dependence of this antelope on water availability (see 7.1.2.1.). Bushbuck habitat selection in relation to water resources was not examined in this study, largely for the same reasons as given above for edge, but the extensive drainage lines at Weza (Fig. 2.2) indicate that few bushbuck home ranges were far from permanent water supplies. This need not imply a dependence on such areas however. The only published study of bushbuck habitat utilization in relation to water availability has been by Simpson (1974a, 1974c) who stated that these antelope "appear to be dependent on its occurrence". Because bushbuck concentrated in habitats adjacent to perennial water sources during the dry season, but dispersed during the rains when surface water was available elsewhere, Simpson (1974a, 1974c) suggested that "the limiting factor governing seasonal dispersal and concentration was the availability of surface water". I consider this to be an extremely spurious interpretation and a classic example of the researcher failing to demonstrate unequivocally the functional significance of factors governing habitat selection, because the bushbuck Simpson studied may well have been responding to changes in food resources. Simpson (1974c) dismisses this by the simple statement that "food plants were spread over most habitats throughout the year". But what of changes in phenology and the seasonal availability of different plant parts available to bushbuck, as well as seasonal differences in forage quality, and seasonal variations in the availability of suitable cover, not to mention competitive interactions with other species etc.? It is highly probable that these factors also influenced habitat utilization and preferences of bushbuck, but these have been ignored by Simpson (1974a, 1974c). Bushbuck were never seen drinking at Weza, nor did proximity to water appear important in Waser's (1975a) study, while bushbuck can survive in areas where surface water is not available for several months (see 7.1.3.1.). These findings therefore suggest that Simpson (1974a, 1974c) has overemphasised the importance of surface water. As a consequence he may well have been responsible for the emphatic statements regarding the dependence of this species

on water resources that persist in the literature (e.g. Wynne-Jones 1980; Rautenbach 1982; Smithers 1983) but that have yet to be substantiated. An equally probable explanation of why bushbuck are associated with water courses and drainage lines may be due to the vegetation such areas provide as both food resources and suitable cover for concealment during the day.

All the above discussions on cover have referred to its importance in providing food, concealment against predators and security from human disturbance. However, numerous studies in North America and Europe have demonstrated the value of cover to cervids in providing shelter against climatic and weather influences and Irwin and Peek (1983) and Loft et al. (1984) have used the term "thermal cover" to differentiate between this and "hiding" or "escape" cover which usually consists of younger trees with less canopy closure. In northern latitudes, where climatic conditions are much more extreme than in South Africa, ungulates frequently use sheltered conifer-dominated habitats where snow depths are substantially less than in more open habitats (Ozoga 1968; Telfer 1970, 1978; Krefting 1974b; Wetzel et al. 1975; Kearney and Gilbert 1976; Peek et al. 1976; Burns 1977; Singer 1979; Armstrong et al. 1983; Brusnyk and Gilbert 1983; Fruzinski et al. 1983; Jenkins and Starkey 1984; Monthey 1984; Pierce and Peek 1984). Although such areas may provide less forage (Ozoga 1968) it may be energetically less costly to remain in these sheltered habitats and fast rather than to forage in more exposed areas (Kearney and Gilbert 1976; Staines 1976; Nudds 1980; see also Chapter Four). Nevertheless, not all habitats with closed canopies have sparse understories, and old-growth forest (uneven age with trees up to 1 000 years old) are particularly important or even essential winter areas for deer in providing both shelter and forage (Bloom 1978; Schoen et al. 1981; Rose 1982; Schoen and Kirchhoff 1985). Even in the absence of snow, many ungulate species seek shelter from the cold winds, and such behaviour may strongly influence habitat selection (Cumming 1966 cited in Lockie 1967; Peek 1971 cited in Peek et al. 1976; Staines 1974, 1976, 1977; Mitchell et al. 1977).

Because closed canopy plantations of conifers can have narrow thermal ranges, warmer internal temperature and reduced wind flow (Verme 1965 cited in Lockie 1967; Ozoga 1968; Bruns 1977; Telfer 1978 cited in Armstrong 1983; Venter 1979), these may be heavily utilized by cervids during cold weather, (Verme and Ozoga 1971 cited in Kearney and Gilbert 1976; Ozoga and Gysel 1972) to minimise radiant and convective heat loss (Moen 1968a, 1968b both cited in Ozoga and Gysel 1972).

Although snow falls did not extend down in to the plantations at Weza, but were confined to the mountain range, sub-zero temperatures were frequently recorded during census operations in winter. Some evidence, albeit circumstantial, indicates that bushbuck may well have sought refuge from these low temperatures and wind chill by selecting densely structured or closed canopy habitats. At night, thickets were more preferred by bushbuck males during winter than at other times of the year, and conversely exposed clearfelled areas were least preferred at this time. Marked temperature inversions occurred at Weza during winter nights, with some low lying habitats as much as 8°C colder than habitats on higher ground. (These temperatures were recorded during censuses and were taken from the road whenever animals were observed. The observed range of -1,0°C to 7,0°C was not influenced by temporal differences and occurred in both June and July when mean census temperatures were 4,3°C and 7,8°C respectively.) Habitats at lower elevations (e.g. riparian zones and poplars) were also generally avoided during winter nights by both males and females; the rejection of riverine areas was particularly pronounced. Conversely, bushbuck might be expected to make greater use of open habitats on sunny winter days as this would reduce thermal stress. Although no such pattern of selection was obvious, (except male preference for grassland in spring), the numerous roads and tracks may have provided higher solar radiation compared to the forests. Finally, it is highly probable that "hiding" cover was also used to provide thermal relief from increased temperatures and solar radiation during the hot summer months.

One other aspect that may have influenced habitat selection by bushbuck concerns the disposal of slash from clearfelling, cleaning, thinning and pruning. This was invariably heaped into parallel continuous rows, approximately 3-5 m apart. The height and width of the slash pile was largely dependent on the productivity of the compartment and the intensity of the management action; but slash piles in excess of 2,0 m wide and 1,5 m high were recorded in some habitats. In addition to reducing the availability of ground layer forage, such slash may well have restricted bushbuck use of plantations, as has been noted for deer in the northern hemisphere (Wallmo 1969; Wallmo and Schoen 1980 cited in Parker et al. 1984). Even when smaller piles of slash did not provide a physical barrier to movement through a compartment, bushbuck may still have avoided such sites; Lyon (1976) cited in Parker et al. (1984) and Lyon and Jensen (1980) found that slash depths in excess of 0,5 m substantially suppressed elk and deer use of clearcuts (both these cervids are significantly larger than bushbuck). Parker et al. (1984) calculated energy costs of locomotion by mule deer and elk through slash and concluded that these were sufficiently high to be a factor clearly favouring slash avoidance. The general pattern of established pine plantation avoidance exhibited by bushbuck may therefore have been due in part to a reluctance to enter compartments where slash was prevalent.

In summary numerous factors undoubtedly influence habitat selection by bushbuck at Weza, the most obvious and easy to assess being the availability of food and cover. Other factors, less easy to define or interpret in ecologically meaningful terms, may be equally important at certain times of the year. Although the functional significance of these parameters is treated independently for convenience, it is highly unlikely that the animal isolates any of these factors in its choice of habitat. It is evident that deer do not necessarily occupy areas with the best of any one commodity, but are generally found where there is the best combination of all the factors influencing dispersion (e.g. Verme 1965 cited in Ozoga 1968; Staines 1974; Suring

and Vohs 1979). Bushbuck clearly respond in the same way in terms of their general pattern of habitat selection, seeking areas where forage and cover (providing concealment as well as a comfortable ambient microclimate) is locally available. Intensive management of small even-aged stands of timber varying from highly productive and diverse early seral stages to mature plantations ensures that a variety of successional stages are locally available to bushbuck. These, intermingled with unmanaged but protected habitats, are undoubtedly responsible for the relatively high densities of this antelope (see Chapter Nine) in what is, after all, an artificial environment. The general habitat of Weza is similar to that proposed for deer wintering areas by Verme (1965) cited in Lockie (1967). Ways in which the habitats at Weza may be manipulated to the benefit of both bushbuck and duiker are proposed in Chapter Ten.

b) Comparisons with other studies of bushbuck habitat selection in forested areas.

Odendaal (1977) studied habitat selection patterns of bushbuck in Forestry plantations of the southern Cape, the results of which were published in Odendaal and Bigalke (1979b). Habitat preference indices were calculated for five bushbuck that were radio tracked for periods varying between 12 days and three months, hence seasonal differences were not examined, nor were all animals monitored at the same time. Vegetation was classified into seven habitat categories which are summmarised in Table 7.16; some of these were similar to categories used at Weza. Odendaal and Bigalke (1979b) concluded that the most preferred habitat was indigenous forests and that habitats offering cover were most preferred during the day while open areas were used extensively at night. This study at Weza corroborates these findings. However, Odendaal and Bigalke (1979b) claimed that lateral cover without canopy cover was totally unattractive during the day yet two of the four marked bushbuck in their study showed H.P.I's greater than 1,0 for this type of habitat. They also concluded that bushbuck showed an extreme avoidance

of gums (but two of four animals utilizing this habitat showed day time selection) and warned of the implications of planting areas with eucalypts where bushbuck populations were desirable. Such an avoidance was not demonstrated in this study, and their recommendations cannot be supported. A possible reason for these differences may have been due to the methods of analysis employed by Odendaal and Bigalke (1979b). Habitat availability was determined from each individual home range, but mean preference indices were used for comparative purposes without any attempt to transform the data to more equal ranges of avoidance and preference. Furthermore, inspection of the original data in Odendaal (1977) unfortunately revealed several inconsistencies and anomalies in his analyses and conclusions (also see Odendaal and Bigalke 1979b; Odendaal et al. 1980). For comparative purposes and using Odendaal's (1977) raw data, mean ranked values of preference and avoidance were calculated following Johnson's (1980) method (Table 7.16). Analysed in this manner, the five bushbuck from the southern Cape apparently showed the greatest overall preference for pine plantations with little understory, particularly during the day, while clearfelled sites devoid of any lateral cover and young plantations were the most preferred habitats at night (Table 7.16). Gums were selected more at night than during the day, but there was no obvious avoidance of these trees as claimed by Odendaal and Bigalke (1979b). Perhaps even more surprising, Odendaal's (1977) data suggest that the bushbuck he monitored avoided indigenous forest during both day and night while grassland areas were consistently the most avoided habitat in his area. Thus preferences determined from a ranking procedure differed markedly from those based on % use:% availability ratios presented in Odendaal and Bigalke (1979b). Although there were some similarities in selection patterns of bushbuck from the southern Cape and from Weza when data were analysed in the same way, there were also some notable differences, particularly with respect to indigenous forests, grasslands and mature plantations. Greater similarities may have been evident had Odendaal (1977) monitored more bushbuck for longer durations.

TABLE 7.16 Diurnal and nocturnal habitat selection patterns of bushbuck in the southern Cape (raw data from Odendaal 1977) as determined from Johnson's (1980) mean ranking method.

D A Y		N I G H T		T O T A L *	
Habitat **	$\bar{x}$ rank value	Habitat	$\bar{x}$ rank value	Habitat	$\bar{x}$ rank value
E	2,50	D	0,90	E	1,38
C	0,90	G	0,63	D	0,80
G	0,38	E	0,50	C	0,10
D	-0,50	C	0,40	G	0,00
A	-0,50	B	-0,40	A	-0,30
B	-0,80	A	-0,70	B	-0,50
F	-1,40	F	-1,10	F	-1,20

* - Total exceeds sum of day and night locations for three of the five bushbuck monitored.

** - Habitat types :

A = indigenous forest

B = immature pines (7 - 9 years) forming an overstory with dense herbaceous undergrowth

C = recently planted pine plantations, trees 1 - 2 m tall

D = clearfelled sites not yet planted with pines, no cover

E = mature and immature pine plantations (18 - 53 years) with very little understory

F = open areas with a high incidence of graminoids near to human habitation, and cultivated areas

G = gum plantations of varying age.

c) Duiker

Attempts to identify the functional significance of habitats selected or avoided by duiker were severely hampered by inadequate numbers of marked animals seen and/or tracked on a minimum of 10 occasions and by disparate proportions of locations recorded during the year, which were greatest in spring and least in summer (Fig. 7.8). Furthermore, efforts to monitor this species by radio tracking were largely unsuccessful, with the result that utilization patterns were based mainly on field observations at night. Consequently assessments of habitat selection were probably biased due to the limitations associated with this method of data collection, and should therefore be interpreted with caution.

The most striking difference between duiker and bushbuck patterns of selection at Weza was the obvious rejection of densely structured habitats by duiker, which was evident for both indigenous and exotic vegetation. Since duiker ventured into habitats with closed canopies, this reluctance to exploit thickets, forest and riverine areas is presumably due to the extensive lateral or ground cover prevalent in these habitats. Avoidance of such areas may have lessened during daylight hours, but the absence of any sign (spoor, faecal pellets or visual contact) of duiker in indigenous forests or dense thickets throughout the course of this study indicates that such habitats were consistently avoided.

The marked preference for oaks, Mexican hawthorns and cultivated areas shown by duiker was probably in response to the localised food resources available in these habitats at certain times of the year. This conclusion is supported by the fact that the majority of animal locations were recorded at night, when duiker spent twice the time feeding that they did during the day (Chapter Eight). Selection for Mexican hawthorns may have been even more pronounced than that recorded in Table 7.13 since, of the 14 duiker caught in this habitat (on a total of 19 occasions) during winter and spring, only 4 of these (29%) were included in data analysis (none of the remaining 10 individuals were relocated on a

minimum of 10 occasions). This stand of trees may also have provided suitable cover for day time use as well; such cover was not available under oaks of in cultivated areas. Seasonal trends in selection could not be determined due to inadequate sampling, but census data indicate that grassland was preferred by duiker throughout the year. In most areas, except those recently burnt or heavily grazed by domestic livestock, grassland would have provided adequate cover for duiker as well as some forage (e.g. forbs and patches of bramble, see Chapter Six) for much of the year. Since oaks, hawthorns and cultivated land were not abundant at Weza but were confined to small, discrete areas available to relatively few duiker, grassland was probably of much greater importance to this antelope overall.

As with bushbuck, selection patterns of marked duiker suggest that plantation areas generally were not preferred habitats of this species, particularly where these were disturbed through intensive management. Nevertheless data from rumen analysis indicate that duiker obtained much of their food requirements from these exotic areas (e.g. bugweed fruits, fungi; the latter were largely confined to areas under mature pines). Other fruits and forbs were common in clearfelled sites and duiker probably utilized these areas for both foraging and cover. Compartments of older (14-18 year) pines were the most preferred timbered areas, and the reduced ground vegetation in these stands may have been more suitable to duiker in providing both cover and some forage. Younger (3-8 year) pines were generally less preferred, but would have contained some of the commodities included in the 14-18 year pine habitat. Duiker showed the greatest avoidance of the next successional stage of pines, and since bushbuck also generally avoided such areas, this rejection may have been related to the more intensive management given to these 9-13 year compartments. By virtue of their smaller size, duiker may also have been more reluctant to enter areas where slash impeded travel. The rejection of poplars by duiker was somewhat surprising, as unmarked animals were observed in young compartments even when these were enclosed by electric fences. Furthermore,

the species composition and density of the understory in mature poplar compartments often resembled that found under 14-18 year pines. However, more intensive and uniform sampling throughout the year may have demonstrated seasonal differences in habitat selection and thus facilitated interpretations of the functional importance of poplars and many of the other habitats.

In summary, the limited data obtained during this study indicate that duiker showed a distinct preference for habitats with reduced lateral cover. These were commonly open areas or habitats where canopy cover restricted but not eliminated understory growth. With the exception of grassland, such habitats at Weza consisted largely of exotic vegetation, from which duiker obtained much of their diet (see Chapter Six). In addition, the range of visibility in these preferred habitats was much less impaired by vegetation than those selected during the day by bushbuck. This range of visibility would facilitate observations of intruding conspecifics (see Chapter Eight) as well as detection of predators. Duiker frequently lie down and hide when disturbed or approached by a predator and only flee when the animal or human is in close proximity (Leuthold 1977); such a response would be largely ineffective if visual contact with the predator was not maintained during this time. Habitat selection by duiker may therefore be influenced by antipredator behaviour in a similar way to that suggested for bushbuck (Waser 1975a) although the actual strategies of predator avoidance and habitat selection patterns adopted by these two largely solitary species show considerable differences.